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JOURNAL OF ANATOMY

ORIGINALLY THE JOURNAL OF ANATOMY AND PHYSIOLOGY

CONDUCTED ON BEHALF OF THE ANATOMICAL SOCIETY OF GREAT BRITAIN AND IRELAND BY

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LINCOLN'S-INN-FIELDS, LONDON, W.C.2

VOLUME LXVI
PART III
APRIL 1932

Entered at New York Post Office as Second Class Matter

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CAMBRIDGE UNIVERSITY PRESS
LONDON: FETTER LANE, E.C. 4
also
H. K. LEWIS & CO., LTD., 136, GOWER STREET, LONDON, W.C. 1
CHICAGO: THE UNIVERSITY OF CHICAGO PRESS
(AGENTS FOR THE UNITED STATES)
BOMBAY, CALCUTTA, MADRAS: MACMILLAN & CO., LTD.
TOKYO: MARUZEN COMPANY, LTD.

Price Ten Shillings net

PRINTED IN GREAT BRITAIN

BIOMETRIKA

A Journal for the Statistical Study of Biological Problems

Shortly: Volume XXIV, Parts I and II. 25s. net (including postage)

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THE EFFECTS OF STIMULATION OF THE HYPOTHALAMIC PUPILLO-DILATOR CENTRE AFTER SUCCESSFUL ANASTOMOSES BETWEEN THE CERVICAL SYMPATHETIC AND CERTAIN MOTOR NERVES

By JOHN BEATTIE, M.D., D.Sc., ARTHUR B. DUEL, M.D., F.A.C.S. and Sir CHARLES BALLANCE, K.C.M.G., LL.D., M.S., F.R.C.S.
New York and Montreal

INTRODUCTION

In a previous paper, one of us (Ballance(1)) described a series of experiments in which the central end of the severed cervical sympathetic trunk was united to the peripheral end of either the hypoglossal, the descendens hypoglossi or the facial nerve. It was shown histologically that the axones of the sympathetic fibres became continuous with the larger nerve fibres in the somatic nerves and that the smaller sympathetic fibres were not continued into these nerves except for a short distance peripheral to the anastomosis. The power of the anastomosis to carry an impulse generated by Faradic stimulation central to the anastomosis was tested. It was found that where scar tissue had not intervened between the segments of the anastomosis and where histological continuity was proved later, the anastomosis could transmit nervous impulses. It was noted that in some animals apparently normal voluntary movements of the musculature supplied by the peripheral nerve took place as early as three months after the anastomosis had been made. It remained, however, to demonstrate whether or not impulses, arising within the brain and which are normally transmitted through the sympathetic nervous system, could pass through the anastomosis and produce effects on the musculature supplied by the peripheral nerve.

Beattie, Brow and Long (2) produced evidence to show that the true sympathetic nervous system (the thoraco-lumbar outflow of Langley) was controlled to some extent by impulses passing from the region of the hypothalamus along a certain pathway in the brain stem and the spinal cord. During the course of their experiments they confirmed the observations of Karplus and Kreidl (3) that stimulation of the hypothalamus can produce pupillo-dilatation. The former observers noted that such dilatation took place in animals whose adrenal glands had been removed. Further unpublished experiments by one of them (Beattie) showed that the pupillo-dilator pathway was uncrossed and that stimulation of a small circumscribed area in the hypothalamus could produce such a dilatation which lasted only as long as the stimulus was applied,

and therefore was not dependent upon the discharge of adrenalin in animals whose adrenal glands were intact.

It seemed to us, therefore, that stimulation of the pupillo-dilator centre in the hypothalamus, under direct observation, might provide a method to determine the functional continuity or otherwise of a cervical sympathetic-somatic nerve anastomosis. Thus contraction of the muscles supplied by the somatic nerve which had been severed would demonstrate beyond doubt the establishment of a new "final common pathway" to the muscles. Also observations on the animals after regeneration had taken place would provide additional evidence to determine the possibility of "voluntary" control through the new path. Observations on the animals during periods of emotional disturbance would show, if the anastomoses were functional, whether or not discharges of nervous energy along the normal pupillo-dilator paths would produce muscular contractions on the side of the operation and pupillo-dilation on the opposite side. Assuming the truth of Bard's statements (4) that "sham rage" depends on the integrity of centres above the decerebration level, then the work of Beattie, Brow and Long (2) would seem to prove that such centres are located in the hypothalamus, and consequently the presence of the phenomena of simultaneous pupillo-dilation and muscular activity taking place on opposite sides of the body during emotional disturbances in animals with a cervical sympathetic-somatic nerve anastomosis would be presumptive evidence that normal discharges from the hypothalamus are causing such phenomena.

METHODS

Fourteen animals were prepared in which the cervical sympathetic trunk was severed and the central end united by an end-to-end anastomosis to the peripheral end of certain severed somatic nerves. After the lapse of a certain length of time, varying from 92 days to 309 days, the cervical sympathetic trunk was exposed in the neck in some of the animals and was stimulated central to the anastomosis by a faradic current to determine the condition of the anastomosis. At a later date the animals were anaesthetised and a hemi-decerebration performed. The whole of the cerebral hemisphere on the side opposite to the anastomosis was removed and the lateral wall of the third ventricle exposed from the opening of the cerebral aqueduct to the level of the infundibular recess (fig. 1).

For the anastomosis operation and the stimulation of the cervical sympathetic trunk ether anaesthesia was used. For the decerebration experiments, the anaesthetic was di-allyl-barbituric acid and urethane in the form of "Dial."

Unipolar electrodes were used for the faradic stimulation of the peripheral nerves and the hypothalamus. The indifferent electrode was sewn under the skin of the lower part of the back.

All the animals used were cats.

CONTROLS

A series of control experiments was performed in which there had been no surgical interference with the nerves in the neck. The hypothalamus was exposed in several cats and in three *Rhesus* monkeys. Stimulation of the proper region gave a constant result—dilatation of the pupil on the side stimulated. There was never any dilatation of the pupil on the off-side to that stimulated in the control or experimental series.

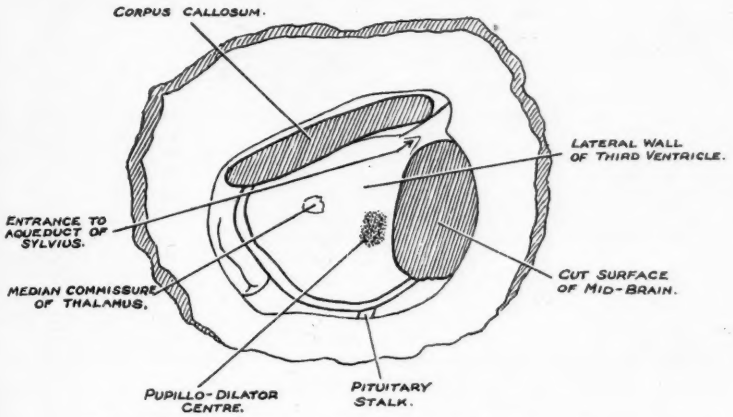

Fig. 1. Diagram of site of pupillo-dilator centre in the hypothalamus.

Table I

Cat No.	Peripheral nerve used	Anastomosis tested at end of	Time in days of period between first operation and hypothalamic stimulation	Effects of hypothalamic stimulation	Remarks
1	Hypoglossal	240 days	254	Contraction of tongue musculature	—
5	„	—	323	„	—
9	„	178 days	178	„	Anastomosis tested after excision of tongue and nerves
2	Descendens hypoglossi	209 „	224	Contraction of sterno-thyroid	Sterno-thyroid and sterno-hyoid contracted with Faradic stimulation of cervical sympathetic
3	Phrenic	173 „	199	Contraction of right half of diaphragm	The animal was examined fluoroscopically(173 days)
4	„	173 „	—	—	Examined fluoroscopically (173 days). Died before hypothalamic stimulation attempted

Table I (*continued*)

Cat No.	Peripheral nerve used	Anastomosis tested at end of	Time in days of period between first operation and hypothalamic stimulation	Effects of hypothalamic stimulation	Remarks
6	Facial	309 days	309	Contraction of facial muscles	Vago-sympathetic stimulation caused contraction of facial muscles (309 days)
10	„	—	230	„	—
7	Superior laryngeal	—	226	Movement of right vocal cord independent of left cord	—
11	„	155 days	155	None	Contraction of right cricothyroid on stimulation of right cervical sympathetic
12	„	155 „	155	„	Effects as in cat 11
8	Glosso-pharyngeal	231 „	231	Elevation of right wall of pharynx	Effects of cervical-sympathetic stimulation identical with hypothalamic stimulation effects
14	„	35 „	—	—	Died when under examination at end of 35 days
13	Inferior laryngeal	154 „	154	None	Sudden adduction of vocal cords on stimulation of cervical sympathetic. Right cord moved more briskly

Table II. *Experiments in which hypothalamic stimulation was attempted*

Anastomosis	Experiments giving positive results on stimulation	Recovery time of positive experiments	Experiments giving negative results on stimulation	Recovery time of negative experiments
Hypoglossal	3	254 323 178	—	—
Descendens hypoglossi	1	224	—	—
Phrenic	1	199	—	—
Facial	2	309 230	—	—
Glosso-pharyngeal	1	231	—	—
Superior laryngeal	1	226	2	155 155
Inferior laryngeal	—	—	1	154

PERSONAL OBSERVATIONS

Cat 1

31*st July*, 1930. ***Operation* (*right side*).**

(*a*) Cervical sympathetic (central end)—hypoglossal (peripheral end) end-to-end anastomosis.

(*b*) Hypoglossal (central end)—cervical sympathetic (peripheral end) end-to-end anastomosis.

The results following the operation were:

(1) Typical signs of cervical sympathetic paralysis.

(2) Paralysis of the right half of the tongue.

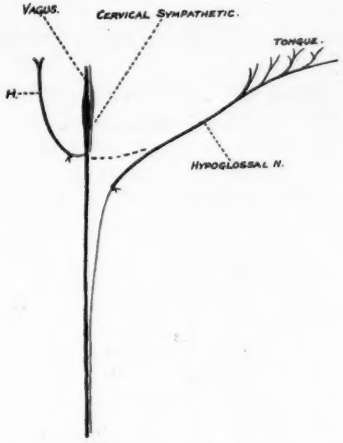

Fig. 2. Diagram of operation. Cervical sympathetic—hypoglossal end-to-end anastomosis. Hypoglossal—cervical sympathetic end-to-end anastomosis.

28th March, 1931. 240 *days*.

No enophthalmos; pupils equal; whiskers on both sides at same level; nictitating membranes retracted equally. Tongue showed no deviation when lapping milk. Right side of tongue was not atrophied. Stimulation by Faradic current caused sides of tongue to respond equally. Faradic stimulation of the vago-sympathetic in the lower part of the neck (right side) produced a ripple of muscular contraction which spread along the right side of the tongue.

11th April, 1931. 254 *days*.

Stimulation of the pupillo-dilator centre in right hypothalamus produced no dilatation or any movement of the right pupil. There was definite contraction of the muscles of the right side of the tongue with every stimulation of the pupillo-dilator centre. The contractions were most marked in the posterior half of the right side of the tongue. The tongue and both hypoglossal nerves were removed together. The right hypoglossal nerve was followed as far as the anastomosis, and beyond this 7 cm. of the cervical sympathetic was removed. The tongue and nerves were then pinned on cork, and bathed with warm saline solution. On stimulating successively (*a*) the proximal end of the cervical sympathetic (right side), and (*b*) the proximal end of the left hypoglossal, the ripple of muscular contraction, which appeared along one side of the tongue, was of equal strength to that on the other side.

Cat 2

30*th August*, 1930. *Operation.*

(*a*) Cervical sympathetic (central end)—descendens noni (peripheral end) end-to-end anastomosis (right side).

(*b*) Descendens noni (central end)—cervical sympathetic (peripheral end) end-to-end anastomosis (right side).

Following the operations, the usual ocular and other signs produced by severance of the cervical sympathetic were observed.

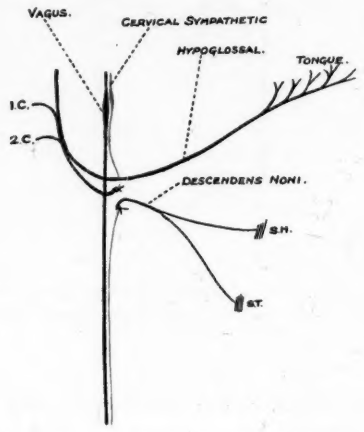

Fig. 3. Diagram of operation. Cervical sympathetic—descendens noni end-to-end anastomosis. Descendens noni—cervical sympathetic end-to-end anastomosis.

28*th March*, 1931. 209 *days.*

Vago-sympathetic exposed and stimulated in the lower part of the right side of the neck. The sterno-hyoid and sterno-thyroid muscles contracted. The enophthalmos, the small pupil, the prominence of the nictitating membrane, etc., have disappeared.

12*th April*, 1931. 224 *days.*

The sterno-hyoid and sterno-thyroid muscles were exposed. On stimulation of the pupillo-dilator centre in the right hypothalamus (unipolar stimulation was used) the right sterno-thyroid contracted rhythmically in a series of tonic contractions during the period of stimulation. There was a marked after-discharge which continued for about thirty seconds. No other muscles contracted during stimulation. The stimulation caused no movement of the pupil on the right side. The sterno-hyoid did not contract; it was much mixed up with scar tissue, and possibly had its nerve damaged.

Cat 3

25th September, 1930. *Operation.*

(*a*) Cervical sympathetic (central end)—phrenic (peripheral end) end-to-end anastomosis (right side).

(*b*) Phrenic (central end)—cervical sympathetic (peripheral end) end-to-end anastomosis (right side).

The phrenic was found on the anterior scalene muscle and three roots were demonstrated coming from each of the 5th, 6th and 7th cervical nerves. No further root of the phrenic nerve was seen. After the operation the ocular signs following division of the sympathetic in the neck were observed. No contraction of the right half of the diaphragm could be felt on palpation of the upper abdomen.

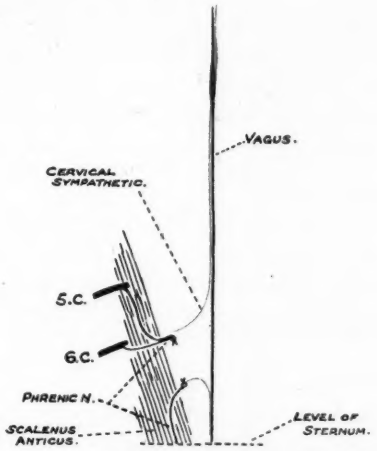

Fig. 4. Diagram of operation. Cervical sympathetic—phrenic end-to-end anastomosis. Phrenic—cervical sympathetic end-to-end anastomosis.

17th March, 1931. 173 *days.*

Dr F. M. Law kindly examined the cat with the fluoroscopic screen in the X-ray department of the Manhattan Ear, Eye and Throat Hospital.

Left half of the diaphragm moved normally. The inner one-third of the right half contracted, but the contraction was not synchronous with the contraction of the left half. The contraction of the inner third of the right half appeared as a wave-like motion. The contraction started on the right side and spread to the left side. During tranquil respiration the outer two-thirds of the right half was straight and did not contract. When the cat cried both halves of the diaphragm became equally depressed, and moved upwards together to their original position.

12*th April*, 1931. 199 *days*.

The right pupil was still a little smaller than the left. Stimulation of the pupillo-dilator centre in the hypothalamic area was carried out with the weakest possible current and with a unipolar electrode. Direct inspection and palpation of the inferior surface of the diaphragm revealed a tonic spasm on the right side synchronous with the moment of stimulation. There was no effect produced on the left side of the diaphragm. During stimulation of the pupillo-dilator centre the diaphragm contracted and remained in this condition on the right side, but normal movements continued on the left side. During the whole period of the experiment breathing continued normally even when stimulation was being applied to the brain. The stimulation did not affect the depth, rhythm or rate of the respiratory movements. The stimulation did not cause any dilatation of the right pupil.

Cat 4

25*th September*, 1930. *Operation*.

(*a*) Cervical sympathetic (central end)—phrenic (peripheral end) end-to-end anastomosis (right side).

(*b*) Phrenic (central end)—cervical sympathetic (peripheral end) end-to-end anastomosis (right side).

A few days after the operation it was noticed that the ocular signs, due to division of the cervical sympathetic, were well marked and that the whiskers drooped on the right side. Further inspection and palpation of the upper part of the abdominal wall clearly demonstrated that the right half of the diaphragm was paralysed.

14*th March*, 1931. 170 *days*.

The ocular signs had completely disappeared with the exception that the right pupil was still very slightly smaller than the left. The right whiskers no longer drooped. On palpation of the upper abdomen no difference could be detected between the contractions of the right and left halves of the diaphragm.

17*th March*, 1931. 173 *days*.

The cat was examined on this date with the fluoroscopic screen at the Manhattan Ear, Eye and Throat Hospital by Dr F. M. Law. Both halves of the diaphragm contracted equally and synchronously. There was no marked difference in the amplitude of contraction or relaxation between the two sides.

28*th March*, 1931. 184 *days*.

The animal died while a dissection in the lower part of the neck was being done. Hence stimulation of the sympathetic centre in the hypothalamus was not attempted. The phrenic nerve was followed on both sides into the thorax. On the right side the cervical sympathetic proximal to the anastomosis and on the left side the phrenic nerve in the neck were submitted to Faradic

stimulation. On both sides the contractions of the diaphragm were equal and vigorous.

Cat 5

3rd September, 1930. *Operation.*

(*a*) Cervical sympathetic (central end)—hypoglossal (peripheral end) end-to-end anastomosis (right side).

(*b*) The peripheral end of the sympathetic was not anastomosed to another nerve.

23rd July, 1931. 323 *days.*

When lapping milk the tongue showed no deviation. The right side of the tongue looked normal and gave a good Faradic response. All ocular signs of cervical sympathetic paralysis were still present, but the whisker hairs had returned to almost the same level as those of the opposite side. Stimulation of the pupillo-dilator centre in the right hypothalamus caused a wave-like tonic contraction of the muscles of the posterior third of the same side of the tongue. The anterior one-third of the right side of the tongue also showed a definite slight tonic contraction which did not occur in the anterior part of the left side of the tongue. The right pupil was not affected by the stimulation in any way.

Cat 6

23rd September, 1930. *Operation.*

(*a*) Cervical sympathetic (central end)—facial (peripheral end) end-to-end anastomosis (right side).

(*b*) The peripheral end of the sympathetic was not united to another nerve.

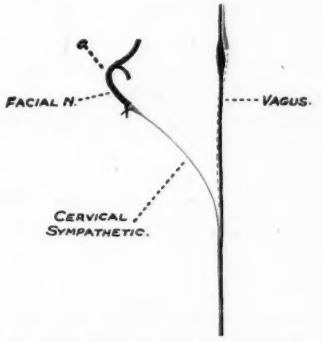

Fig. 5. Diagram of operation. Cervical sympathetic—facial end-to-end anastomosis. Cervical sympathetic (peripheral end) not anastomosed to another nerve.

28th July, 1931. 309 *days.*

The muscles of the face reacted to the Faradic current. Stimulation of the vago-sympathetic (right side) above the sternum produced contraction of the

muscles of the face. Stimulation of the pupillo-dilator centre in the right hypothalamus caused closure of the right palpebral fissure, elevation of the angle of the mouth, slight contraction in the muscles of the upper lip and movement of the whiskers. The right pupil did not dilate. On this date there were noted, enophthalmos, right pupil small, the membrana nictitans prominent, and the whisker hairs drooped.

Cat 7

8th December, 1930. *Operation.*

(*a*) Cervical sympathetic (central end)—motor part of superior laryngeal (peripheral end) end-to-end anastomosis (right side). The motor part of the superior laryngeal nerve was dissected free of the sensory portion and divided near the ganglion of the trunk of the vagus.

(*b*) The cervical sympathetic (peripheral end) was united (end to side) to the lower border of the hypoglossal nerve.

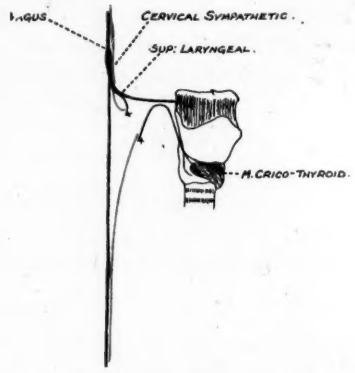

Fig. 6. Diagram of operation. Cervical sympathetic—superior laryngeal (motor part) end-to-end anastomosis. Superior laryngeal (motor part)—cervical sympathetic end-to-end anastomosis.

14th March, 1931. 96 *days.*

It was noted that the ocular signs had completely disappeared, and that the whisker hairs no longer drooped.

22nd July, 1931. 226 *days.*

On examining the vocal cords the right cord was seen not to be so tense as the left. During stimulation of the pupillo-dilator centre the vocal cords were observed through the direct laryngoscope and later by splitting the thyroid cartilage. At the moment of stimulation the right cord was seen to straighten independently of the left cord (under normal circumstances both cords move together, as they do when the "centre" for the abduction and adduction of the vocal cords in the Rolandic cortex of the opposite side

of the brain is stimulated). The cords were (during stimulation) also observed to come together with a snap, the right cord being straight and tense. The right pupil did not dilate during this stimulation. Unfortunately the observation of the right cricothyroid muscle was not satisfactory. Later, it was seen to be like the left cricothyroid muscle. There was no atrophy and it reacted like the left muscle to direct Faradic stimulation.

Cat 8

9th December, 1931. *Operation.*

(*a*) Cervical sympathetic (central end)—glosso-pharyngeal (peripheral end) end-to-end anastomosis (right side).

(*b*) The peripheral end of the sympathetic was not united to another nerve.

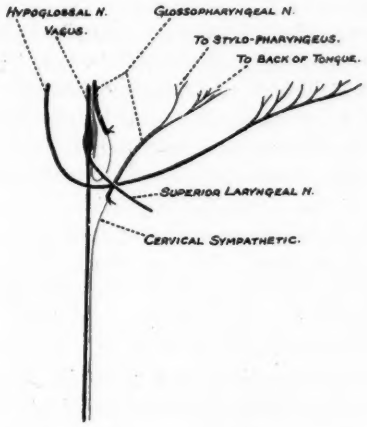

Fig. 7. Diagram of operation. Cervical sympathetic—glosso-pharyngeal end-to-end anastomosis. Glosso-pharyngeal—cervical sympathetic end-to-end anastomosis.

14th March, 1931. 95 *days.*

All the signs produced by the severance of the cervical sympathetic were present.

28th July, 1931. 231 *days.*

The ocular and other signs of cervical sympathetic paralysis were observed. The right cervical sympathetic was exposed and stimulated in the lower part of the neck. The effect of stimulation was elevation of the right wall of the pharynx. Stimulation of the pupillo-dilator centre in the right hypothalamus caused the right pharyngeal wall to be drawn upwards and outwards. The right pupil was not affected by the stimulation.

Cat 9

11*th December*, 1930. *Operation.*

(*a*) Cervical sympathetic (central end)—hypoglossal (peripheral end) end-to-end anastomosis (right side).

(*b*) The hypoglossal was followed to the base of the skull and there divided.

(*c*) The peripheral end of the sympathetic was not united to another nerve.

14*th March*, 1931. 93 *days*.

The tongue was not deviated when lapping milk. The signs caused by division of the sympathetic showed no indication of recovering.

7*th June*, 1931. 178 *days*.

Present: Dr Learmonth of Rochester, Dr Mackenzie of Toronto, and Dr Cone of Montreal.

The tongue on inspection did not show any atrophy on the right side. On stimulation of the pupillo-dilator centre in the right hypothalamus the posterior third of the right side of the tongue showed a tonic contraction of the muscles. The right pupil was unaffected by the stimulation. The tongue and hypoglossal nerve were removed together. On the right side the dissection included the cervical sympathetic-hypoglossal anastomosis together with several centimetres of the sympathetic proximal to the anastomosis. The tongue and nerves were pinned on a sheet of cork and bathed in warm saline solution. The right hypoglossal distal to the anastomosis appeared to be slightly smaller than the left hypoglossal. Faradic stimulation of the right sympathetic proximal to the anastomosis and of the left hypoglossal produced a ripple of muscular contraction along the corresponding side of the tongue. At first these contractions were equal in strength, but later, those on the left side were stronger than those on the right.

Cat 10

12*th December*, 1930. *Operation.*

(*a*) Cervical sympathetic (central end)—facial (peripheral end) end-to-end anastomosis (right side).

(*b*) The peripheral end of the sympathetic was not united to another nerve.

14*th March*, 1931. 92 *days*.

There was no improvement in the signs caused by division of the sympathetic.

30*th July*, 1931. 230 *days*.

The signs of cervical sympathetic paralysis were still present. Stimulation of the pupillo-dilator centre in the right hypothalamus gave rise to elevation of the right angle of the mouth and the right upper lip. There was almost

complete closure of the palpebral fissure. The pinna moved in an antero-posterior plane.

Cat 11

24th February, 1931. *Operation.*

(*a*) Cervical sympathetic (central end)—superior laryngeal, motor part (peripheral end)—end-to-end anastomosis (right side).

(*b*) Superior laryngeal sensory part (central end)—cervical sympathetic (peripheral end) side-to-end anastomosis (right side).

29th July, 1931. 155 *days.*

Examination of vocal cords by the laryngoscope showed that the right cord was slack and its abduction excursion was less than that of the right cord in tranquil respiration. The cricothyroid muscles were exposed and the vocal cords brought into direct view by splitting the thyroid cartilage. On Faradic stimulation of the right cervical sympathetic proximal to the anastomosis and of the anastomosis itself the following effects were noted:

(1) The right cricothyroid contracted.

(2) The right vocal cord straightened and came up against the left vocal with a snap; the tension of both cords at this moment was equal.

The stimulation of the pupillo-dilator centre in the hypothalamus was negative.

On the above date the notes say that no one of the signs caused by the division of the sympathetic is present.

Cat 12

24th February, 1931. *Operation.*

(*a*) Cervical sympathetic (central end)—superior laryngeal nerve (peripheral end) end-to-end anastomosis (right side). In this case the section of the sympathetic was through the middle of the superior cervical ganglion.

(*b*) The peripheral end of the sympathetic (superior cervical ganglion) was not united to another nerve.

29th July, 1931. 155 *days.*

The results of stimulation of the cervical sympathetic and the hypothalamus were similar to those observed on cat 11 on the same date, except that, though no surgical anastomosis had been done, the "eye signs" caused by the division of the sympathetic had almost disappeared. In this experiment the superior cervical ganglion was divided and *not* the trunk of the nerve. Previous experience had shown that when the ganglion was cut through and the peripheral end of the sympathetic ganglion was not united by surgical means to another nerve, recovery of the ocular signs was more probable than when the section passed through the trunk of the sympathetic.

Cat 13

26th February, 1931. *Operation.*

(*a*) Cervical sympathetic (central end)—recurrent laryngeal (peripheral end) end-to-end anastomosis (right side).

(*b*) The peripheral end of the sympathetic was not united to another nerve.

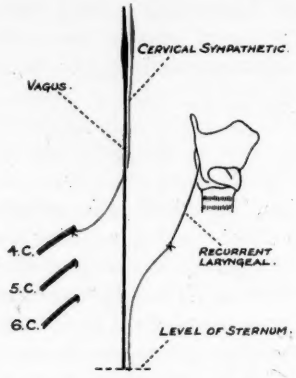

Fig. 8. Diagram of operation. Cervical sympathetic—recurrent laryngeal end-to-end anastomosis. 4th cervical nerve (anterior primary division)—cervical sympathetic side-to-end anastomosis.

30th July, 1931. 154 *days.*

Dissection of neck. The cervical sympathetic in the lower part of the neck and the anastomosis were exposed. Observation of the vocal cords through direct laryngoscope showed that in tranquil respiration the movements of the vocal cords were normal. Faradic stimulation of the cervical sympathetic proximal to the anastomosis and of the anastomosis itself caused sudden adduction of the vocal cords. The movement of the right cord was more brisk than that of the left cord. (It should be remembered that the adduction movement is more powerful than the abduction movement.) The stimulation of the pupillo-dilator centre in the hypothalamus caused no movement of the vocal cord. On this date it was noticed:

(1) That the voice of the cat was normal.

(2) That the signs caused by division of the sympathetic were still present.

Cat 14

27th February, 1931. *Operation.*

(*a*) Cervical sympathetic (central end)—glosso-pharyngeal motor part (peripheral end) end-to-end anastomosis (right side). The motor part of the glosso-pharyngeal was separated from the sensory part almost as high as the petrous ganglion and then divided.

(*b*) The peripheral end of the sympathetic was not united to another nerve.

Some time later (5 weeks) the cat died during an examination under ether. The stimulation of the sympathetic centre in the hypothalamus was not attempted. The sympathetic nerve proximal to the anastomosis and the anastomosis were exposed and stimulated with the Faradic current.

Result: the right wall of the pharynx moved a little upwards and laterally. At the time of death the signs caused by the severance of the cervical sympathetic were well marked.

DISCUSSION

Twelve of the fourteen animals on which anastomosis had been performed had the pupillo-dilator centre in the hypothalamus stimulated. Nine animals showed contraction of muscles within the region supplied by the peripheral nerve used for the distal segment of the anastomosis. The three negative results occurred in animals which had survived for 154 (1) and 155 (2) days. The shortest period of recovery in the positive experiments was 178 days (cervical sympathetic-hypoglossal, cat 9). As so many factors must be taken into consideration it is impossible to be certain that successful hypothalamic stimulation required a recovery period greater than 155 days and less than 178 days. It must be mentioned that in all the unsuccessful hypothalamic stimulation experiments the anastomosis was able to transmit nervous impulses excited by Faradic stimulation of the cervical sympathetic central to the anastomosis.

Stimulation of the pupillo-dilator centre produced effects which were similar to those brought forth by stimulation of the nerve trunk central to the anastomosis. In one animal (cat 2) a prolonged after-discharge lasting almost thirty seconds was observed after each hypothalamic stimulation. This phenomenon was not seen when the nerve trunk was stimulated. The hypoglossal anastomosis showed a ripple-like wave of contraction passing from back to front over the side of the tongue but most marked in the posterior region. In the descendens hypoglossi experiment (cat 2) the contraction of the sterno-thyroid muscle was definitely rhythmic. The experiment on the animal with a phrenic nerve anastomosis (cat 3) demonstrated a tonic spasm of the diaphragm with each hypothalamic stimulation and synchronous with the stimulation period.

The two phrenic nerve experiments (cats 3 and 4) differed from each other in the fluoroscopic appearances. Cat 4 showed no dissimilarity in the activity of the two halves of the diaphragm. There was synchronous movement of each half. In cat 3 during tranquil respiration the inner third of the affected half of the diaphragm showed a ripple-like contraction which appeared just before the normal side contracted. The outer two-thirds of the affected side remained inactive. When the animal cried both sides moved synchronously and to the same extent. In other words all the muscular units on the affected side were thrown into action during the emotional disturbance. The significance

of these observations cannot be doubted. Both animals had survived 173 days from the time of the anastomosis operation. One showed not only complete recovery from the operation but synchronous activity with the other half of the diaphragm. The other animal demonstrated synchronous activity only under emotional stress. It is difficult to see what the nervous pathways could have been which effected the simultaneous contraction of both halves of the diaphragm, but that a mechanism for this phenomenon was elaborated cannot be gainsaid.

The animals with hypoglossal anastomoses showed recovery from tongue deviation when lapping milk as early as the 93rd day. Recovery from cervical sympathetic paralysis was observed at the 96th day when the peripheral end of the cervical sympathetic had been united at the operation to the central end of the severed somatic nerve. Normal movements of the vocal cords were observed at the 154th day after suture of the recurrent laryngeal nerve to the central end of the cut cervical sympathetic. Motor recovery is apparently quite rapid in cervical sympathetic-peripheral nerve anastomosis.

It has been mentioned above that simultaneous contraction of the two halves of the diaphragm was present at about the 173rd day. The experiment (cat 3) which showed these synchronous movements only during emotional disturbance may suggest a possible route for the *motor* impulses through the hypothalamus and the descending tracts described by Beattie,, Brow and Long (2), but none of our experiments throw any light on the possibility of the recovery of a proprioceptive nervous mechanism within the originally paralysed muscles. We have demonstrated bilateral synchronous muscular movements within 180 days after a successful anastomosis, but such movements do not require for their execution a proprioceptive reflex mechanism as is required for the "stretch" reflex of Sherrington. The nature of the activity of the hypothalamus under normal conditions is unknown. That it does control the secretion of adrenalin (Houssay and Molinelli (5)) and consequently the level of blood sugar in the body (Cori and Cori (6)) is not sufficient evidence to justify the assumption that it exerts a "tonic" influence on the sympathetic nervous system. The work of Cannon (7) and Bard (4) would seem to indicate that the hypothalamus and the sympathetic nervous system are essential parts of a mechanism employed during certain emotional conditions to maintain the internal environment of the individual at a constant level. Rioch (8) has shown that the hypothalamus is connected intimately to certain thalamic nuclei, and it is conceivable that by such thalamic connections sensory impulses may be able to re-establish new pathways within the central nervous system and effect contraction of striped muscle under the conditions we have described in our experiments.

SUMMARY

1. A series of experiments is described in which the central end of the severed sympathetic trunk was anastomosed to the peripheral end of a cut motor nerve in the neck.

2. Recovery of muscular activity was noted in all animals allowed to survive for a period varying from 154 to 323 days.

3. Stimulation of the pupillo-dilator centre in the hypothalamus produced the same type of muscular activity as stimulation of the cervical sympathetic trunk proximal to the anastomosis, in animals surviving from 178 to 323 days.

4. Evidence that motor impulses reach the paralysed muscles as early as the 93rd day is recorded.

We have to acknowledge our indebtedness to the Carnegie Foundation, the Millbank Memorial Foundation and the Lillian Babbitt Hyde Foundation and several private friends for generous support of the work on which this paper is founded.

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A STUDY BY DEGENERATION METHODS OF THE INNERVATION OF THE MUSCLES OF A LIZARD (*EGERNIA*)

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Muscle of lizards and snakes is remarkable for the variety of form of the nerves and nerve endings that supply it. This innervation has been subjected to many careful studies. In a paper written in 1882, Bremer (6) published his admirable investigations; by means of the gold chloride method he demonstrated three types of nerves supplying the muscle fibres: (*a*) coarse medullated fibres, (*b*) fine medullated fibres, (*c*) non-medullated fibres. Type (*a*) ended in hypolemmal branching terminations; or in "plate-like" forms, resembling those of mammals; or occasionally in many knobs ("Doldenförmige Endigungen" of Bremer; "terminaisons en grappes" of Tschiriew). By general consent these nerves are regarded as somatic motor. Types (*b*) and (*c*) end in simple or more complex "terminaisons en grappes," and they have been the subject of much discussion. Bremer stated that they were hypolemmal, and regarded them as sensory, Sherrington's demonstration of the sensory function of the spindle fibres having not yet been given. Perroncito (28)[1] and Stefanelli (32) considered them a modified type of somatic motor fibre, but subsequently took them for sympathetic. Tschiriew (33), Kühne (21), and von Thanhoffer (37) regarded them as immature motor nerves. Wilkinson (38) has recently inclined to this view, without inferring, however, that they will necessarily ever become mature; some he thinks are probably sensory. Kulchitsky (23) and Dart (10) examined them in *Python* muscle, and believed they were sympathetic nerves, the latter author distinguishing sympathetic sensory and sympathetic motor nerves. Boeke (4, 5) concluded that many of the "terminaisons en grappes" are modified forms of the ordinary motor endings, since, as Perroncito had also observed, they may at times be the endings of thin non-medullated collaterals of coarse medullated fibres, which themselves end in typical motor plates. But there are many fibres for which this is not the case; they may arise from finely medullated fibres, or, as Bremer found, never become medullated, at any rate as far as it is possible to trace them in the preparations. Boeke suggests that some of these may be sensory nerves, others possibly sympathetic.

The present paper is based on a study of lizard muscle in which the components of the nerves to the muscles have been identified by degeneration tests. The result of these experiments has been to show that the coarse fibres and the

[1] I have not had direct access to the Italian literature here quoted.

fine medullated and unmedullated fibres that end on the muscle fibres by "terminaisons en grappes" arise from cells in the grey matter of the cord, and are therefore presumably somatic motor fibres; that the muscle spindle is supplied by at least two fibres, one of dorsal root origin, the other arising in the spinal cord; and that the sympathetic fibres supply the blood vessels alone.

Such tests are rendered necessary by the fact that it is really quite impossible to determine the origin of fine nerve fibres by the presence or absence of a medullary sheath; for, as Langley showed (24), many post-ganglionic sympathetic fibres may be weakly medullated, while many fibres that are only finely medullated occur in the ventral roots (25).

METHODS AND MATERIAL

The animal employed in this study was *Egernia cunninghamii*, a form of large "sleepy lizard" occurring commonly in south-eastern Australia, the adults attaining somewhat over a foot in length. The intercostal, leg, and tail muscles were examined, and to these muscles alone do the subsequent remarks apply.

The relevant anatomical facts were first determined in some preliminary dissections. In the nerves to the intercostal muscles the spinal ganglia lie well outside the spinal column, just proximal to the point of junction of the two nerve roots; the common nerve trunk then passes downwards and bends under the rib, where it receives a single fine ramus from the sympathetic ganglion at a distance of about 8 mm. from the dorsal root ganglion. The sympathetic nerves were isolated by severing the nerve trunk proximal to the junction with the sympathetic ramus, about 1 mm. beyond the spinal ganglion. Five (or six) successive nerves on one side were thus cut, the middle (or middle two) segments alone being examined after degeneration had occurred; the latter precaution seemed necessary in view of possible overlapping of nerves from adjacent segments. The greatest care was taken to avoid cutting the fine sympathetic rami. Post-mortem examinations were made to confirm the operation, but reliance was especially placed upon subsequently finding the sympathetic nerves intact in places where they are known to occur (blood vessels).

The sensory nerves may be completely degenerated, leaving sympathetic and motor fibres intact, by removing the spinal ganglia; these ganglia are so closely placed to the common nerve trunk that, as subsequent histological examination showed, a considerable destruction of motor fibres also occurs. However, many motor fibres remain intact, so that qualitative results, which alone were sought, are not thereby affected.

To isolate the sympathetic fibres to the hind leg, the spinal column was opened over an appropriate length, and the five nerves to the hind limb severed inside the spinal canal, the dorsal roots being pulled in till the spinal ganglia also could be destroyed. By this more difficult operation alone did I find it possible to destroy the spinal nerves to the leg, leaving the sympathetic fibres intact.

The tail region is particularly well adapted for these experiments, for the spinal cord may be completely destroyed here, without seriously affecting the

animals while in captivity. The spinal ganglia are placed well outside the spinal canal, at the entrance to the intervertebral foramina; the sympathetic chain may be traced a considerable distance into the tail, below the vertebral column. The somatic motor nerves may therefore be destroyed by entirely removing the spinal cord, either by first opening the spinal column and drawing out the cord in one piece, or by the simple procedure of snipping off the tip of the tail, and forcing a piece of wire of suitable thickness to the required length along the spinal canal. Sensory and sympathetic nerves are left intact. To destroy sensory nerves also, the spinal ganglia must be located and removed after exposing the cord. A period of several months is required for complete degeneration of all severed nerves.

The following material was then prepared:

Animal A. Large lizard. Spinal cord of tail destroyed; 57 days' degeneration of somatic motor fibres. Sensory and sympathetic fibres intact.

Animal B. Very young lizard (5 inches long). Spinal cord of tail destroyed; 65 days' degeneration. Sensory and sympathetic fibres intact.

Animal C. Fully grown lizard. Five successive intercostal nerves cut proximal to junction with rami; 70 days' degeneration. Sympathetics alone intact.

Animal D. Large lizard. Motor and sensory innervation of right hind leg degenerated for 102 days. Sympathetics alone intact.

Animal E. Fully grown lizard. Five successive sensory ganglia to intercostal muscles removed; 116 days' degeneration. Sympathetic fibres intact; somatic motor fibres partly intact.

Animal F. Fully grown lizard. Somatic nerves to five successive intercostal segments severed just distal to sensory ganglia; 138 days' degeneration. Sympathetics alone intact.

Animal G. Fully grown lizard. Somatic nerves to six successive intercostal segments severed distal to sensory ganglia; 146 days' degeneration. Sympathetic fibres alone intact.

Animal H. Adult lizard. Spinal cord of tail and sensory ganglia removed; 165 days' degeneration. Sympathetics alone intact.

The degeneration was carried out mainly in warm weather; during cooler periods the animals were artificially warmed.

At the end of the period of degeneration the tissue was prepared either by the Bielschowsky or the gold chloride method. From animals *A*, *B*, *F*, *G*, *H*, both types of preparation were made; from *C*, *D*, *E* only Bielschowsky preparations.

Of the two methods the gold technique yields the more instructive preparations, for it is possible to trace in the teased material individual nerve and muscle fibres for very great distances; it has the further advantage that it usually shows fine sympathetic fibres on blood vessels with great clearness. The Bielschowsky technique is much more capricious; it cannot be relied upon to show sympathetic fibres, but when it does so, they usually stain very sharply. The necessity of using sections rather than teased material has great disadvan-

tages; it is also much more difficult to distinguish fine medullated from unmedullated fibres, though even with the gold method this may be difficult enough. The interpretation of the pictures yielded by these methods, and also by the methylene-blue process, which I have used for unoperated material, is discussed below.

OBSERVATIONS ON THE INNERVATION OF *EGERNIA* MUSCLE

Bundles of nerve fibres, entering the muscle, separate into smaller bundles, which may unite with other small bundles; but eventually there emerge from the tracts of nerves the individual fibres which, with or without further branching, end, after a shorter or longer path, in connection with the muscle fibres.

A. *Coarse medullated fibres*

Of the fibres that thus emerge singly from the bundles the most striking are the coarse medullated fibres that form end-organs on the muscle tissue. They are obviously somatic motor nerves, and in animals *A* and *B* they are found, without exception, in advanced stages of degeneration, while sensory and sympathetic fibres are intact.

Detailed study of the composition of the motor end-organ reveals a structure that does not agree in all respects with that commonly described in the literature.

(i) *Continuity of sheath of Henle with the sheath of the muscle fibre.* As the coarse nerve fibres emerge from the smaller nerve bundles, the perineural sheath of Henle that encases these bundles is continued on to them as a fine transparent tubular sheath that accompanies them to their termination on the muscle fibres. Here it becomes directly continuous with the sheath that invests the muscle fibre.

By most authors this sheath of Henle is mistaken for the neurolemma (sheath of Schwann); and it is stated incorrectly that the neurolemma is continuous with the sarcolemma. In case there be any doubt as to the correct identification of the tubular sheath within which the isolated nerve fibres run, the following features which distinguish it from the neurolemma may be stated: (*a*) it is found investing single nerve fibres only when these have emerged from the bundles, not when they are within the bundles; (*b*) it is directly continuous with the sheath of Henle that invests the bundle as a whole; (*c*) it does not exhibit constrictions at the nodes of Ranvier; (*d*) its nuclei are irregularly placed and do not correspond with the internodal segments of the nerve fibre. These observations may readily be made on the living tissue or in gold preparations (Plate I, fig. 7); Bielschowsky material is less suitable, since the sheath undergoes much distortion.

The neurolemma is most difficult to detect. In Bielschowsky preparations I have never seen it. In gold preparations axon and myelin sheath usually stain very deeply, and are not individually distinguishable; nor are neurolemma and its nuclei then visible. But in less deeply stained fibres the axon can be seen

enveloped in weaker staining myelin, on the outer margin of which the nuclei of the neurolemma are now visible (Plate I, fig. 7). Even then the neurolemma can only be seen where it is raised from the myelin by its nuclei. It is sometimes also to be seen as a very delicate membrane stretching across fractures in the myelin substance. The neurolemmal cells are best to be seen in a modified form in fibres that have undergone Wallerian degeneration. As is well known, axon and myelin then entirely disappear, whilst the neurolemmal cells transform themselves into long syncytial columns, the so-called cords of Büngner (see Boeke (2)), encased by the apparently unaltered perineural sheath of Henle (Plate I, fig. 10).

The statement that neurolemma is continuous with sarcolemma was first made by Kühne (19). The correct relationship was known to Ranvier (29). Kühne subsequently admitted that he had mistaken the sheath of Henle for neurolemma; but while agreeing with Ranvier that the sheath of Henle became continuous with the sarcolemma, he believed that the neurolemma had a similar relationship (20). His evidence is purely indirect and unconvincing. Direct observation of motor end-organs in strict profile lends no support to his contention.

In the foregoing description I have avoided the conclusion that the sheath of Henle is continuous with the *sarcolemma*, as there seems to be some uncertainty also in the identification of this membrane; this is discussed below in connection with muscle spindles (see p. 316, footnote 1). At present it is merely concluded that Henle's sheath which encases the nerve bundles encases also the individual nerve fibres that emerge from these bundles, and becomes continuous with a sheath that closely invests each muscle fibre.

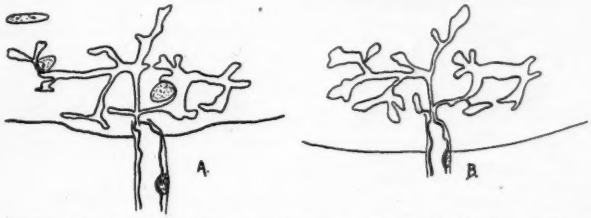
(ii) *The end ramification of the axon.* Within the "eminence of Doyere," and beneath the investing sheath (telolemma of Kühne), the axon expands into the well-known terminal arborisation. Gold chloride and methylene-blue preparations yield very similar pictures of this structure; in Bielschowsky preparations they appear entirely different, and one is apt to ask which, if any, of these pictures has an objective value.

Over sixty years ago Kühne observed that it was sometimes possible to see the nerve terminals in living *Lacerta* muscle. In the muscles of *Egernia* this is also sometimes possible. When a suitable muscle such as the sartorius is examined fresh in saline, the coarse medullated fibres can be seen with perfect clearness as they emerge from the nerve bundles; in most cases they can be followed right up to their ending on the muscle, then suddenly, when the myelin sheath stops, they too seem to end, and of the arborisation nothing whatever is visible. But in some cases one becomes vaguely aware of the faint outlines of this structure. Among these are some in which the form of the arborisation can be seen with tolerable clearness; and after the eye has become accustomed to their excessively pale and dim outline it even becomes possible to draw them with some accuracy . In Plate I, fig. 9, is shown an example of such an end-organ; even the sole-plate protoplasm is visible, together with several nuclei.

It will be seen that the structure is very similar to that with which we are familiar in gold and methylene-blue preparations.

For purposes of accurate control it is necessary to compare the appearance of a single nerve ending fresh and then stained. Accordingly an end-organ was selected whose outlines could be seen with some accuracy and then rapidly sketched. The tissue was now immersed in methylene blue and in due time the ending appeared stained. Drawings of the living and stained ending are shown in text-fig. 1. The differences on the left portion of the ending are due to the fact that it was not possible to place the structure in quite the same position as in the fresh tissue. It is clear, however, that the stain has given a fairly faithful reproduction of the original living structure. The general picture of the end-organs as seen in gold and methylene-blue preparations is, as above remarked, very similar; and since it is easy to select many almost perfect replicas in the two forms of preparation, it was not deemed essential to carry out the technically much more difficult control of a gold-stained ending.

The end-organ as revealed by the Bielschowsky method differs markedly from that shown by the gold or methylene-blue process. Usually the branches

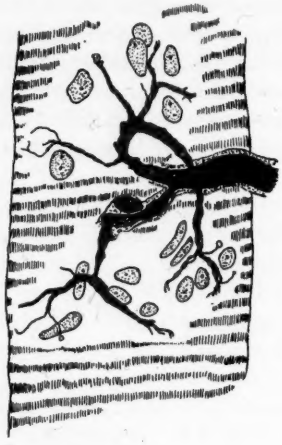


Text-fig. 1. Outline drawing of a coarse motor nerve ending. A. Living. B. The same ending stained *intra vitam* with methylene blue. The two drawings have been unavoidably made in slightly different positions.

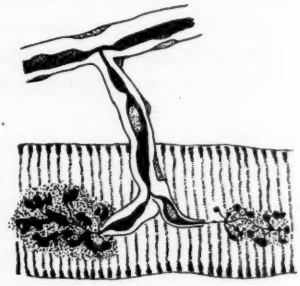
are long and slender and give off finer twigs (text-fig. 2). Often it is possible to resolve the branches into several constituent neurofibrils. Occasionally coarser endings are seen, composed of numerous very delicate fibrils (text-fig. 2). The excellent illustrations of Boeke (3) of similar endings from *Tropidonotus* muscle may be referred to. Plainly the Bielschowsky method does not reproduce the appearance of the living nerve ending. Is the difference to be ascribed to distortion or to selective staining of only a component of the end-organ? The following observations suggest that the latter is probably the case.

In examining the living end-organs, and before its possible interpretation was appreciated, I occasionally noticed a dark line running like an axis through the whole organ and its branches (Plate I, fig. 9). Subsequently I have found several records in the literature of such an axial structure, always from methylene-blue preparations. It was first described by Dogiel (11) in 1890, subsequently by Feist (12) and Kulchitsky (22), and it is often to be seen in methylene-blue preparations of *Egernia* muscle (Plate II, fig. 13). Evidently it is a definite component of the end-organ.

These observations suggest that this axis represents the fibrillar portion of the end-organ and that, while the methylene-blue process often stains both fibrillar and perifibrillar substances, the gold method reveals only the latter, the silver method only the former. This explanation is rendered the more probable by the fact that it can be definitely shown in the more complex types of ending (text-fig. 2) that the fibrils alone impregnate, for the spaces between the fibrils remain clear and colourless. But, be the explanation what it may, it seems plain that a recent criticism by Lawrentjew (26) that the gold method fails to reveal the true form of the nerve ending and "yields unquestioned artefacts," and that it is much inferior to the Bielschowsky methods can hardly be justified.



Text-fig. 2.



Text-fig. 3.

Text-fig. 2. Very coarse medullated nerve, forming two end-organs on a muscle fibre. Bielschowsky method; leg muscle.

Text-fig. 3. Coarse motor nerve, terminating by an end-organ, one half of which is of the "en grappes" type, the other half transitional between this and an "en plaque" form. Gold chloride; leg muscle.

(iii) *Variation in form of the end ramification of the coarse medullated fibre.* The commonest form of this organ met with is the fairly compact type shown in Plate I, fig. 7 (the so-called "plate-like" endings). But much variation occurs. Occasionally very simple forms are seen, where the ending presents but two slightly serrated branches. Very commonly the compact type is replaced by a more spreading form (Plate I, fig. 8), which may undergo various elaborations. Sometimes there occur small twigs that end in knobs, which may be angular or rounded. Sometimes the entire end-ramification may be in the form of an elegant spray of these fine knobs ("terminaisons en grappes"). Sometimes one half of the end-organ may be thus constructed, the other half presenting a typical "plate" structure. Transitional forms also occur (text-fig. 3). Frequently the

nerve divides into two or more branches just before ending on the muscle fibre; some of them may be non-medullated, and they may be enclosed in a common sheath of Henle, or in separate sheaths, or may at times be devoid of such a sheath. In this manner elaborate and complex forms of end-organ may arise. A variety of "terminaisons en grappes" occasionally seen presents the form of a whole cloud of terminal knobs.

The above description is based on an examination of a large series of gold preparations. In Bielschowsky material some of these forms may also be recognised; for example the end-knobs of the gold preparations appear as coarse or delicate loops, evidently because their fibrillar component alone has been impregnated. Many excellent illustrations of these endings by this method are given in Boeke's papers (4,5).

The foregoing remarks apply only to the arbitrarily chosen group of coarse fibres that are medullated as far as, or almost as far as, their endings; in animals *A* and *B* they are all degenerating and are therefore somatic motor fibres.

(iv) *The "perilemma."* In 1887 Kühne described a peculiar component of the motor end-organ frequently visible in gold preparations and sometimes in the living tissue. It occurs as a layer of protoplasm closely following the contours of the more deeply stained end-ramification. He believed it was part of the axon terminal, which was therefore composed of two parts, an inner "axial-baum" representing the neurofibrils of the end-organ, and a supporting perifibrillar substance, which he therefore called the "stroma." It was most clearly to be seen by focussing immediately "below" the "axial-baum"; a further characteristic was a peculiar rod-like or palisade structure of its outer margins, though this was not always clearly visible. This "stroma" may readily be identified in some gold preparations (Plate I, figs. 7, 10), though it often seems to become disorganised. In my experience it may often be seen in methylene-blue preparations (Plate II, fig. 13), and occasionally, and then with great clearness, in Bielschowsky material (Plate I, figs. 11, 12; Plate II, fig. 14).

Kühne's belief that it is part of the axon terminal (perifibrillar stroma), may readily be disproved; for I find that it persists, apparently unaltered, in end-organs in which the axon has completely degenerated (Plate I, fig. 10; Plate II, fig. 14). It is clearly a very definite component of the motor end-organ. I shall speak of it here as the "perilemma" (Gr. *lemma*, a husk), Kühne's term "stroma" being inapplicable.

What are its relationships? Although it is quite distinct from the sole-plate protoplasm, it may be merely a condensation of that tissue. But it is also possible that it is homologous with neurolemmal tissue; for in degenerated end-organs, from which the axon has completely disappeared, the modified neurolemmal cells (cords of Büngner) can now be seen to be in direct continuity with the perilemma. A profile view of any gold-stained degenerated ending shows this clearly (Plate I, fig. 10); it is also to be seen in Plate II, fig. 14, and in the photograph, Plate II, fig. 14 *a*. This cannot be taken as decisive evidence of the

neurolemmal origin of the perilemma, but it suggests its possibility. It will be recalled that no definite ending for the neurolemma has been given in the foregoing description. After the myelin sheath terminates, the neurolemma can sometimes be followed for a very short distance further along the axon, but thereafter is unrecognisable, just as it is invisible on any non-medullated fibre. Unless, then, such a connection becomes established during the process of degeneration, it must follow that the neurolemma merges into the perilemma. But the evidence is not conclusive.

Although it is seen with maximum clearness by focussing just "under" the axon terminal, yet profile views show that it surrounds that structure, though it is thickest "beneath" it. It appears to be devoid of nuclei. That the large, irregularly disposed, sole-plate nuclei lie outside it is easily seen in most preparations (Plate I, figs. 11, 12; Plate II, figs. 13, 14); they may actually project into indentations of its margin, but definitely avoid its substance. Cases where this at first appears otherwise prove on careful focussing to be due to nuclei lying immediately "beneath" the perilemma.

Besides the sole-plate nuclei a second type of nucleus occurs in the end-organs, the telolemmal nuclei of Kühne, lying within the telolemmal sheath that invests the end-organ from above, and forms a transition between Henle's sheath and the sheath of the muscle fibre (Plate I, fig. 10; Plate II, fig. 15). In good Bielschowsky preparations these nuclei stain very deep black, in contrast to the weakly staining sole-plate nuclei; they are also more rounded and smaller. It is a remarkable fact that these nuclei almost always lie in close association with one branch or another of the end-ramification. This fact was known to Ranvier, who believed he could distinguish, in addition to the sole-plate and telolemmal nuclei, a third type, associated with the end-ramification ("noyaux de l'arborisation"). Kühne denied this. The regularity with which these nuclei are associated with the branching ending is striking (Plate I, fig. 11), and at first sight seems to indicate that the nuclei belong either to the perilemma, or what is much less probable, to the axon terminal, as Ranvier thought. But very careful focussing shows that they lie just "above" the axon terminal, and in profile view they are seen to lie in the telolemma, branches of the axon lying immediately below them. Occasionally surface views may be observed (Plate I, fig. 12) where the nuclei are definitely dissociated from the end-ramification. Such cases seem to show that the association is of a purely subsidiary nature and that the perilemma is devoid of nuclei; at any rate in these cases it definitely does not contain them.

The drawing (Plate I, fig. 11) of a nerve terminal with perilemma stained by the Bielschowsky method is so similar to that of a living nerve ending in which the axial structures are visible (Plate I, fig. 9) that suspicion may be felt that what is regarded as living nerve ending really includes also perilemma, and that the Bielschowsky method, despite the foregoing criticism, faithfully reproduces the form of the living nerve ending. The difficulty is a real one, when pictures yielded by different methods are under comparison; for even if methylene blue,

as above described, selectively stains what is regarded as living nerve terminal, is it not possible that it is the perilemma that is being coloured? A complete answer to this criticism is possible. The exasperating caprice of the methylene-blue process is well known to all who have used it. In the motor end-organ it sometimes stains only the end-ramification; at other times the axial structures are visible within this; sometimes only the sole-plate protoplasm colours, and an uncoloured negative of the nerve terminal is then seen. But frequently the perilemma also appears around the margin of the nerve ending, and if numerous examples of freshly stained end-organs are examined, sooner or later a case will be found where axon ramification with its axial structure and with perilemma are visible side by side. An example of such a case, rapidly sketched from a freshly stained preparation, is given in Plate II, fig. 13. The sole-plate is also indicated with a few of the nuclei that were visible, but they were only very weakly stained.

Further control is possible by degenerating the axon end-ramification. For the purpose the sciatic nerve was severed in several lizards, and after a period of 90 days' degeneration methylene-blue preparations of the tissue were made. The axon ramification was found to have completely disappeared, but perilemma and sole-plate protoplasm were still stainable.

(v) *The sole.* On the outside this is invested by telolemma, except where the axon enters it; here its protoplasm seems to be in direct contact with the (fluid?) contents of the tubular sheath of Henle. In profile view a faint granular structure is recognisable in the living protoplasm, as Kühne was the first to observe. In adult animals it may sometimes be pigmented. The sole-plate nuclei lie mostly beneath the end-ramification and are irregularly disposed, differing in this respect from the true muscle nuclei, which all lie with their axes along the length of the muscle fibre.

(vi) *Relation of the nerve terminal to the muscle tissue.* Some years ago I described from a gold preparation of frog tissue fine filaments connecting the nerve terminal with Krause's membrane of the muscle fibre (34). This observation has not, to my knowledge, been confirmed, while several authors have stated their inability to see it. Nevertheless in good preparations, by the gold or Bielschowsky method, it may sometimes be seen with comparative clearness. To make the demonstration more objective I present in Plate II, figs. 15 *b* and *c*, two photographs at different magnifications of a profile view of a nerve terminal taken from a young *Egernia*. Only one branch of the nerve terminal is in focus in the photograph; the fine filamentous connections with Krause's membrane are obvious. In the accompanying drawing (Plate II, fig. 15 *a*) a more complete picture of this end-organ is given, another branch of the nerve terminal being drawn on to the same plane. Doubt may be felt whether the connection is really with Krause's membrane or with the anisotropic substance; it should be explained that the fibre is in a partially contracted condition and that the darkly staining substance, which in the relaxed fibre occupies the anisotropic segments of the fibrils, has accumulated about Krause's membrane (cf. (35)).

Does such a connection exist in all the coarse motor end-organs? Clearly, we have no means yet of deciding this question. The fact that it cannot usually be seen is of little significance; how often is the end-organ itself visible unless it is selectively stained? It would hardly seem that so striking a structural relationship should occur only in some special cases. Can it be an artefact? Again we cannot decide this question; but why should our fixing fluids produce such striking connections in a homogeneous mass of protoplasm? Such an explanation would only create greater difficulties. Nor can shrinkage explain the fact; it can break down such connections, but it can hardly establish them. Of the nature of these connecting filaments, i.e. whether they are extensions of Krause's membrane, or neurofibrillar in origin, nothing can be said.

Having come to the apparently novel conclusion that such connections exist between Krause's membrane and the nerve terminal, I was surprised to find that it had been seen in *Hydrophilus* by Foettinger (13) as long ago as 1880, confirmed two years later by von Thanhoffer (36).

(vii) *Ultraterminal fibres.* Although many hundreds of these coarse nerve endings have been examined, only two cases of true ultraterminal fibres have been seen, i.e. fibres that arise from a hypolemmal end-organ and terminate on another fibre. One of these ended on a spindle fibre, the other on an ordinary muscle fibre. In the latter case the ultraterminal fibre was definitely medullated (Kühne has already figured such a case), in the former case non-medullated.

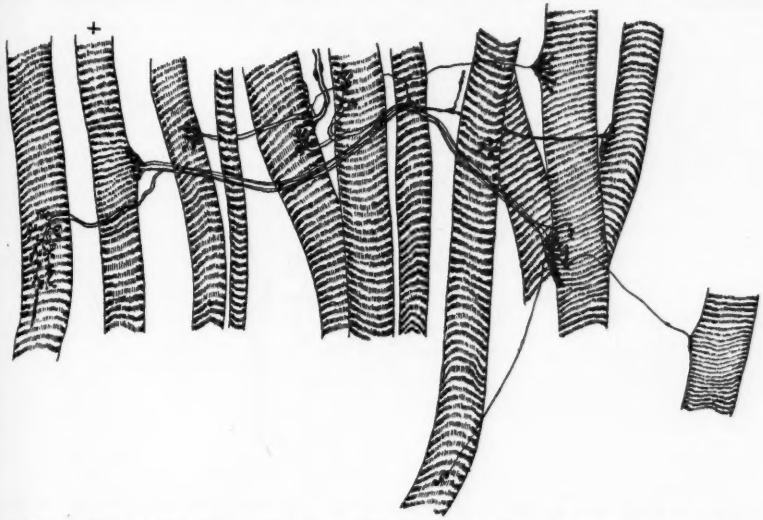
B. *Fine medullated and non-medullated fibres*

In this section are described all the remaining nerves that form end-organs on muscle fibres (exclusive of spindles), i.e. all those fibres which are unmedullated or only weakly medullated for a considerable distance before forming end-organs. It is these nerves that have been the subject of so much discussion recently, and have been variously considered as sensory, sympathetic, immature somatic motor, etc.

In animal *E* (with spinal ganglia removed) they are still seen; they are therefore not all sensory as Bremer thought. In well-stained gold or Bielschowsky preparations from animals *C, D, F, G, H*, in which sympathetic fibres alone are intact, I have never seen them despite long and careful search. Yet in normal unoperated material they can easily be found. I must conclude that none of them can be sympathetic fibres; and must therefore, by exclusion, be somatic motor. The proof that they are all without exception somatic motor is obtained from animal *B* (very young lizard, sensory and sympathetic fibres intact, all somatic motor nerves degenerated, 65 days); in the tail muscle of this animal all the coarse medullated fibres and their motor endings have degenerated; many fine fibres, usually considerably degenerated, are still visible, but their end-plates have completely disappeared. It is therefore possible to identify these nerves in a partially degenerated condition. On the other hand in animal *A* (57 days' degeneration of somatic nerves of large adult) many of the fine fibres with their end-organs are visibly undergoing degeneration; but there are

still many that are not obviously affected; for at least another month would be necessary to degenerate them all in a large adult.

In well-stained gold-chloride material there may be seen, emerging from the nerve bundles, single, very delicate, fibres that after a longer or shorter course form end-organs on the muscle fibres. Sometimes they are quite unmedullated; at other times they exhibit a delicate myelin sheath. A very fine Henle's sheath may invest them for their entire length, or apparently only for a short distance. When traced backwards into the nerve bundles they may sometimes be seen to arise, at a node of Ranvier, from comparatively coarse medullated fibres; at other times they are to be traced for considerable distances along the nerve bundles without apparently becoming medullated; or again

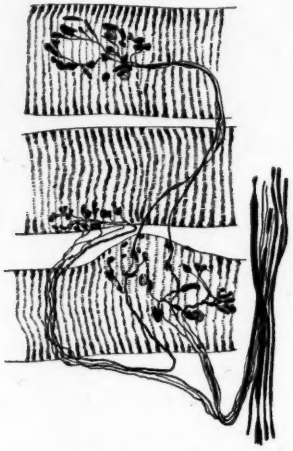


Text-fig. 4. Tract of fine unmedullated nerve fibres traversing the muscle tissue and ending on the fibres by sprays of minute end-knobs ("terminaisons en grappes"). The end-organ on the muscle fibre indicated by + is shown in detail in Plate II, fig. 16. Tibialis anticus; large adult; gold chloride.

they may be found to arise from the tapering off of medullated fibres of considerable thickness. Their origin from medullated fibres does not necessarily disprove their sympathetic origin; for Langley (24) has found that many post-ganglionic sympathetic fibres are medullated. Nevertheless they all degenerate when somatic motor fibres alone are destroyed and therefore arise from the grey matter of the cord. In gold-chloride preparations their endings have the appearance of typical "terminaisons en grappes"; usually the fine fibres divide into several branches that form a spray of end-knobs or bulbs beneath the muscle sheath; but at times there may be only a small number of such knobs, sometimes only one or two.

Complications arise when two or even more nerve fibres enter into the formation of a single end-organ (text-fig. 5); they may arise from the same or from quite distinct nerve bundles; commonly a single finely medullated nerve may be seen to divide into two fine unmedullated branches, which then proceed for a considerable distance side by side, to form eventually a common spray of nerve terminals. A special case of this is seen in Plate III, fig. 18, where the one branch forms a minute ending within the main motor end-organ. The amount of variation is obviously very great.

At times there may be seen, emerging from the nerve bundles, groups of finely medullated or even unmedullated fibres; they do not at first separate, but traverse the muscle tissue as tracts of delicate fibres up to six or even more in number, giving off in their passage fine sprays of "terminaisons en grappes"



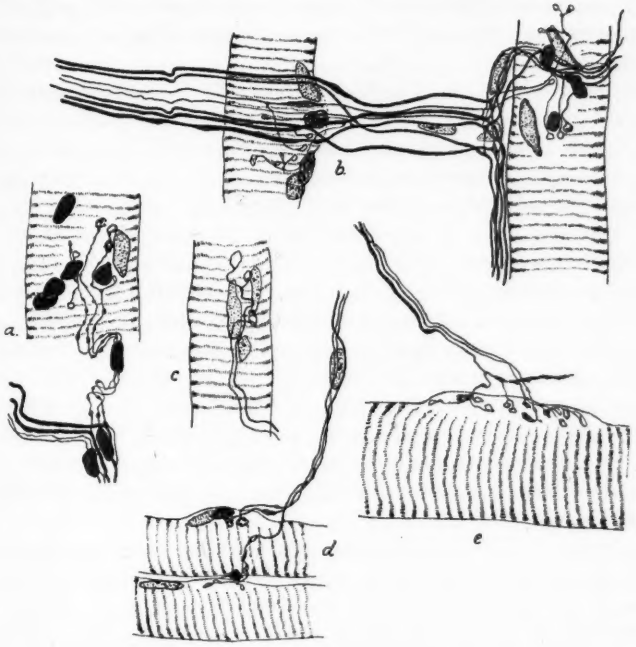
Text-fig. 5. From the small nerve bundle a group of finely medullated and unmedullated fibres emerge and end by "terminaisons en grappes" on three muscle fibres. Note the formation of ultraterminal fibres from one of the three end-organs. Tibialis anticus; gold chloride.

to many of the muscle fibres (text-fig. 4) Sometimes each fibre of the tract, even up to six or seven in number, may contribute to the formation of a single end-organ, so that elaborate and very elegant sprays of minute end-knobs arise. Usually the end-organs are at the terminations of short collaterals from the constituent fibres of the bundle (text-fig. 6 *a* and *b*; Plate II, fig. 16); but quite often the end-organ arises without the formation of collaterals, and then the bundle is continued by the outgrowth of true ultraterminal fibres from the hypolemmal ending (text-fig. 5). A similar condition was described by Bremer (6) for *Lacerta*. Despite their close resemblance to sympathetic fibres these nerves all originate from the spinal cord, for they are not found in material in which somatic motor fibres alone have degenerated.

Apart from the above description further details of the minute structure of

the motor end-organs are difficult to determine, for these endings usually stain less strongly than those of the coarse medullated fibres.

Bremer stated that the endings were hypolemmal; Kulchitsky thought they were epilemmal. In *Egernia* I find that, if seen in perfect profile, they can usually be shown in gold preparations to end under the muscle sheath (Plate III, fig. 20); and although there are many doubtful cases, there are none that one could call definitely epilemmal. Boeke finds that silver preparations are better



Text-fig. 6. Fine unmedullated nerves ending by "terminaisons en grappes" on muscle fibres. In *a* and *b* the origin of some of these fibres from coarser and probably medullated nerves is apparent. In *d* and *e* note the hypolemmal position of the endings and a slight Doyerean eminence. Adult lizard; tail muscle; Bielschowsky preparation.

suited for deciding the question, and states that the endings then appear hypolemmal (4). This I can confirm (text-fig. 6 *d* and *e*).

Whenever it is possible to follow Henle's sheath as far as the end-organ it can be seen in continuity with the sheath of the muscle fibre. Sometimes an "eminence of Doyere" is present (text-fig. 6 *e*), but at other times is scarcely or not at all recognisable. In gold preparations sole-plate protoplasm seldom stains; usually in fact it seems to be quite absent. Boeke found that in silver preparations it could be much better seen; this I can confirm, having never

failed to see it, provided the end-organ could be seen in perfect profile. Sole-plate nuclei can be distinguished from telolemmal nuclei as in the coarse endings; usually they are present in only small numbers, and in some minute endings (Plate III, fig. 19) definitely no nuclei are visible even though they appear in neighbouring parts of the muscle. Whether perilemma is differentiated I am unable to decide. In those cases where the staining is particularly sharp, definite connections between the end-knobs and Krause's membrane can be demonstrated, as in the coarse type of end-organ (Plate II, figs. 16, 16 *a*).

Methylene blue yields similar preparations to those by the gold method. In Bielschowsky preparations the end-knobs appear as delicate loops (text-fig. 6), evidently due to selective fibrillar staining.

According to Bremer's drawings, both in the frog and in *Lacerta*, coarse and delicate fibres may end upon one and the same muscle fibre. But Kulchitsky stated that in *Python* muscle the coarse nerves end only on thick muscle fibres, the fine nerves on thin fibres; and Wilkinson believes that this occurs also in the lizard *Tiliqua*. This is denied by Boeke for *Tropidonotus*. In *Egernia* such a selective innervation of muscle fibres does not occur; on the contrary coarse and delicate nerves may quite often be seen to end upon one and the same muscle fibre; and in gold-chloride material in which the fibres have been adequately isolated for a sufficient length I have occasionally found instances of fibres provided with one or two coarse end-plates and two or three delicate "terminaisons en grappes" (see Plate III, fig. 17). This multiple innervation of single muscle fibres in *Egernia* is sometimes so obvious that the question arises whether a single muscle fibre is ever innervated by one form of nerve alone. But we have no means of answering this question, since it would involve the isolation of the muscle fibres for their entire length, and a complete staining of all the nerves.

The degeneration experiments already described show that these nerves are all somatic motor. Some have regarded them as a distinct form of motor nerve; Tschiriew (33) and Kühne (21) took them for developmental forms. Boeke (5) recently suggested that many of them are merely young forms. Wilkinson (38) has also adopted this view, with the reservation, however, that they may never become mature. But the use of the term "immature" in this sense seems hardly valid. In support of the view that they are immature is the fact that several such fibres may enter into the formation of a single end-organ, which Boeke finds especially common in embryonic tissue. But this conclusion would be difficult to harmonise with the following facts: (i) already in very young animals the two sets of fibres are clearly recognisable, the coarse fibres ending in typical "plates" distinguishable only in size from those of adults; (ii) the fine fibres are just as common in old as in young animals, but the end-organs are usually much larger in the adult. Hence even if forms occur that might be regarded as transitional, there is no reason to believe that the fibres in question will ever develop into typical coarse fibres; (iii) if they were young forms they might be expected to follow the general rule of degenerating earlier than the

coarse, presumably older, fibres[1]. But in animals *A* and *B* the opposite is found to be the case; for while the coarse fibres are all in advanced degeneration, the thin fibres are still largely present, although in animal *B* their end-organs have completely vanished.

C. *The neuromuscular spindles*

These are very common in the limb musculature, less frequent in the intercostal muscles, and only seldom found in the tail. The fibres are exceedingly narrow (17 μ) in their encapsulated region, though outside this they thicken. They are innervated from two sources, from the dorsal root ganglion and from the spinal cord.

(i) *Sensory innervation*. The origin of these fibres was demonstrated by Sherrington by degeneration tests in 1894 (31). His conclusions for the mammal hold also for *Egernia*, for these fibres are not found in animals *C*, *D*, *F*, *G*, *H*, in which sympathetic nerves alone persist, but are intact in animal *B*, where somatic motor fibres alone have degenerated; while in animal *E*, deprived of its sensory supply, they are seen in degeneration.

Most commonly the very coarse (9–13 μ diameter) medullated fibres divide into two at a node of Ranvier, and travel, still as medullated fibres, in opposite directions along the length of the spindle fibre, beneath its capsule, which may consist of several lamellae; sometimes an extension of the sheath of Henle may accompany the sensory nerve after it has entered the capsule, and must not be confused with neurolemma. From the intracapsular fibre there arise at the nodal constrictions collateral branches; they accompany the spindle fibre for some distance, sometimes running in spirals around it, and giving off lateral excrescences that are intimately applied to the spindle fibre (Plate III, fig. 21). They appear thus in gold preparations; in Bielschowsky preparations the nerve fibre appears thinner and its neurofibrils are seen.

Many variations occur. Sometimes the sensory fibre fails to bifurcate on entering the spindle (Plate III, fig. 21). Sometimes it divides into three parts at a nodal constriction. Occasionally two distinct fibres occur, each bifurcating at its entrance to the spindle; or again two spindles may be innervated by branches of one and the same axon.

Sometimes, as Kulchitsky has already described for the *Python*, two distinct spindle fibres may be enveloped within a common capsule, though their extracapsular regions are separate.

(ii) *Motor innervation*[2]. The presence on the spindle fibres of another smaller

[1] For example, Ross Harrison (16) finds that in 6 mm. frog embryos the vagus fibres completely degenerate 5 days after section; with increase in age of larvae the period becomes progressively longer. In adult frogs, as is well known, several months are necessary to ensure complete degeneration.

[2] The presence of this somatic motor nerve suggests that the spindle fibre is contractile, which would in any case follow from its microscopical structure. In isolated frog muscle, but not in lizard muscle, I have seen the spindle fibres undergoing twitching indistinguishable in appearance from an ordinary muscle twitch. The observation is of interest, because it has been suggested that the spindle contraction is of a much more prolonged nature.

nerve was known to Kerschner (18) and Ruffini (30), and has been described by Perroncito, Cajal, Boeke, Dogiel and others. Ruffini, Giacomini (15), and Crevatin (8) took it for sensory. Its somatic motor nature, first suggested by Kerschner, would seem to be conclusively shown by Perroncito's observation that it may arise as an ultraterminal extension of a typical motor end-organ (lizard). Disregarding this fact, Dart (10) maintains that the fibre is sympathetic in origin (*Python*). Boeke (4) on the contrary confirms Perroncito's observation (*Tropidonotus*), and shows experimentally that this nerve alone degenerates when the spinal nerves are cut proximal to the sensory ganglia (cat).

In *Egernia* the origin of this fibre from the spinal cord is readily demonstrated. In animals *C, D, F, G, H* it is either not found, or, if seen, is in advanced degeneration; Dart's statement that it is sympathetic in origin is therefore evidently wrong. It is seen in animal *E*, and is therefore not sensory. In Plate III, fig. 22, is shown a spindle from animal *B* with this fibre in degeneration, while the sensory nerve has persisted.

Both the nerve and its end-organ display much variation. Sometimes the nerve is coarsely medullated, and may pass directly to its ending or give off a collateral that forms a typical motor organ on the spindle fibre. Sometimes the fibre may be very slender and non-medullated, and such a fibre may arise from the bundles of fine nerves that form "terminaisons en grappes" on ordinary muscle fibres. Sometimes several fine nerves terminate at intervals on a spindle fibre. I have seen one case where as many as eleven motor endings could be counted on a single isolated spindle fibre over a length of 1 cm. (tibialis anticus); two of these are shown in Plate III, fig. 23 *a* and *c*.

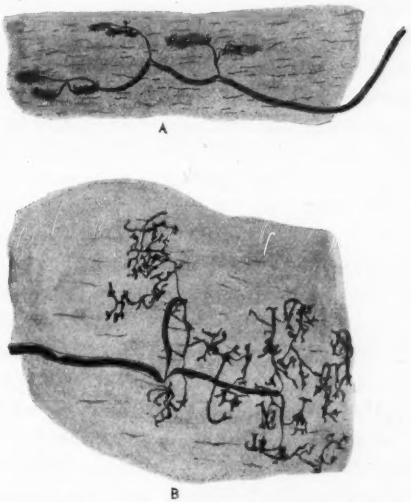
At its termination the accompanying sheath of Henle becomes continuous with the sheath of the spindle fibre[1]. The end-organ varies much in form. Sometimes there is a small spray of rounded knobs of varying degrees of coarseness; at other times the ending may be comparatively large, with thick bosses applied to the muscle fibre (Plate III, fig. 23 *b*). I have not seen a prominent Doyerean eminence.

[1] The sheaths of Henle of the sensory and motor fibre are, as already stated, continuous with the connective tissue capsule and the extracapsular sheath respectively of the spindle fibre. But the capsule becomes very closely applied at its ends to the spindle fibre, and directly merges into a sheath which closely invests that fibre and which is absent as such in the intracapsular region. If seen on an ordinary muscle fibre the extracapsular sheath would be called sarcolemma. Is the sarcolemma of a muscle fibre then derived from the muscle fibre itself, or is it, like the spindle capsule, perimysial in origin? That it contains nuclei distinct from the muscle nuclei has long been known, and this argues for the second alternative, though it is not necessarily inconsistent with the first. There is good evidence that there are really two distinct membranes concerned, (i) a true non-nucleated delicate sarcolemma, derived from the muscle fibre itself, and attached to the telophragmata of the fibre—only certain types of preparation reveal it, and (ii) a coarse nucleated membrane derived from the perimysium, and usually mistaken for true sarcolemma (see Baldwin (1)). It is for this reason that I have avoided the term sarcolemma in this paper. By stating that Henle's sheath is continuous with the muscle sheath I mean a connection with the coarse nucleated membrane that closely invests the muscle fibre, and not with the delicate true sarcolemma, assuming the distinction is valid. According to von Thanhoffer (37) the motor nerve ends between the two sheaths. But if the spindle capsule is homologous with the muscle sheath, are then the sensory nerves of spindles not also "hypolemmal"?

D. *The tendon organs (organs of Golgi)*

In gold-chloride preparations the tendon organs of Golgi may readily be seen; I have found them in the tendons of the tail and leg musculature, and especially in the great tendons of the large back muscles.

Their origin from dorsal root ganglia as in other animals may readily be demonstrated. Thus in animal *B*, with all somatic motor nerves degenerated, they persist; but are not found in animal *D*, deprived of somatic motor and sensory nerves. The fibres are coarse and enveloped in a sheath of Henle. From the nodes of Ranvier there arise usually several collaterals that, after a short distance, develop very characteristic end-organs. These are complex, highly branched, structures that ramify among the tendon fibres; the terminal filaments do not end in knobs, but taper out into short sharp points (text-fig. 24).



Text-fig. 24. Tendon organs of Golgi. A. View, under low magnification, of a single nerve fibre enclosed in a sheath of Henle, forming end-organs amongst the fibrous tissue of the tendon. From a tendon of large back muscle. B. View under higher magnification of portion of Golgi organ. From triceps tendon. Gold chloride.

E. *The sympathetic nerves*

These have been isolated in animals *C*, *D*, *F*, *G*, *H*, by degenerating all somatic nerves. Several months were devoted to a careful search on gold and Bielschowsky material for intact delicate nerve endings on the muscle fibres, but without success; all persisting non-medullated fibres lie in close association with large or small blood vessels, and never form plexuses of fibres that traverse the muscle tissue independently of these. Unless then such a plexus is much more refractory to our staining methods than the sympathetic fibres of blood vessels, its existence in this animal must be denied.

Can a sympathetic innervation of skeletal muscle tissue then be definitely excluded? Such an innervation, did it exist, must be by way of fine unstained collaterals of the vascular nerves. In the absence of physiological evidence for their existence it would be unjustifiable to assume such an innervation. It seems fair comment to assert that all work that has ascribed the maintenance of muscle tone to sympathetic action has failed to withstand critical examination. The experiments of Orbeli provide evidence of a different nature, and seem to show that sympathetic nerves delay by their action the onset of fatigue in even bloodless muscle. Observations which might be similarly interpreted were unexpectedly obtained by Coates and Tiegs (7), though alternative explanations are not here excluded. But recently Maibach (27) has reported experiments which appear to confirm Orbeli's work.

Should Orbeli's effect then exist it would provide strong presumptive evidence for a direct sympathetic innervation of muscle tissue. It is a disconcerting fact in modern histological work that we never see the actual, very delicate, connections between the sympathetic vascular nerves and the plain muscle fibres of the arterioles; and yet presumably such connections exist. It is therefore not impossible that similar nerves, ending on the striated muscle fibres, may provide the anatomical basis for Orbeli's observation, even if present methods fail to reveal them. But there may be another explanation. It may have a purely humoral origin; and one might point to the recent tendency to ascribe the pseudomuscular contracture of de-efferented muscle to such a source (14). Here apparently acetylcholine, liberated at the endings of vasodilator nerves, stimulates the sensitised muscle. Could not then a substance with adrenaline-like properties be liberated at the endings of sympathetic vasoconstrictor nerves? Now recent experiments by Dale and Gaddum (9) suggest that this indeed occurs. In that case, to account for the Orbeli effect, a direct sympathetic innervation of the striated muscle fibres need not be postulated; but it also cannot be excluded. Whatever the ultimate explanation may be, it seems clear that all those delicate nerves that have been observed in reptilian muscle to end on the muscle fibres are merely a system of modified somatic motor nerves.

APPENDIX

The innervation of Python muscle. *Python* muscle has a particular interest, for it was on this tissue that Kulchitsky made the observations on which the late Prof. J. I. Hunter based his theory of muscle tone (17). Kulchitsky thought the fine non-medullated fibres that ended in "terminaisons en grappes" on muscle fibres were probably sympathetic. Dart stated that they were quite definitely sympathetic. Boeke (5) has recently criticised these conclusions; he thinks that most of these fibres are not sympathetic but somatic motor, though some of the very finest may prove to be sympathetic in origin.

Dr C. H. Kellaway, of the Walter and the Eliza Hall Institute, Melbourne, kindly provided me with several live specimens of the Australian carpet snake (*Python spilotes*) upon which these conflicting statements have been tested.

Python material responds extraordinarily well to gold or Bielschowsky treatment, and in the intercostal and tail musculature the two types of fibre described by Kulchitsky are recognisable without trouble. On one of the pythons a degeneration test was then performed. The operation consisted in snipping off the end of the tail and destroying the spinal cord by forcing a piece of wire along the vertebral canal to within about 4 cm. of the cloaca. Sensory and sympathetic nerves are left intact. After 102 days' degeneration part of the tail was removed; the remainder was removed after a degeneration period of 165 days, and the material prepared by the gold and Bielschowsky methods.

In the preparations the degenerated coarse motor endings are numerous; the fine "terminaisons en grappes" have entirely disappeared; sympathetic fibres are found intact on the blood vessels, but never elsewhere; the sensory nerves of the spindles are preserved, but not the fine extracapsular nerve ending; there also persist some very coarse medullated fibres that terminate in the external perimysial tissue by sensory endings resembling the tendon organs of Golgi.

I hope to describe the innervation of this very peculiar tissue more fully later.

SUMMARY

1. By means of degeneration tests the somatic motor, somatic sensory, and sympathetic components of the nerves supplying the intercostal, leg and tail muscles of a lizard have been identified.

2. The somatic motor fibres may be (*a*) coarse medullated, (*b*) fine medullated, (*c*) fine unmedullated. Type (*a*) forms the well-known coarse motor end-organs on the muscle fibres, and their varieties are described. Types (*b*) and (*c*) traverse the muscle either in bundles or singly, and end in fine knobs, usually in the form of elegant sprays ("terminaisons en grappes"). These different types may be found ending on one and the same muscle fibre.

3. The neuromuscular spindles are innervated by a very coarse fibre, terminating within the capsule and originating in the dorsal root ganglion; and by one or more or even many nerves ending in the extracapsular region of the fibre, and somatic motor in origin.

4. Complex branching sense organs (Golgi organs) are found in the muscle tendons; the nerves originate in the dorsal root ganglia.

5. Sympathetic nerves are found only on the blood vessels.

6. The structure of the coarse motor end-organ has been analysed by differential staining and by degeneration experiments. The sheath of Henle (not neurolemma) is continuous with the sheath of the muscle fibre. The axon ramification is composed of an axial (fibrillar) and a perifibrillar substance. The whole is invested by a special component of the end-organ ("perilemma"; "stroma" of Kühne), apparently devoid of nuclei; it persists after axon degeneration. This is surrounded by the faintly granular nucleated sole-plate. The nerve terminals are connected by fine filaments with Krause's membrane of the muscle fibre.

7. Gold chloride and methylene blue are found to reproduce the form of the living axon ramification with considerable accuracy; Bielschowsky preparations apparently stain only its fibrillar elements.

8. Degeneration tests on *Python* muscle show that the sympathetic nerves are found only on its blood vessels, and that all the fine "terminaisons en grappes" are somatic motor nerves.

For the microphotographs which illustrate some of the disputed matter referred to in this paper I am indebted to Dr E. S. J. King, of the Pathology Department, Melbourne University, who has gone to a great deal of trouble to obtain sharp negatives; I am also very grateful to Mr K. C. Richardson, of Sydney, for help with these photographs.

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EXPLANATION OF PLATES

Plate I

Fig. 7. Common form of motor end-organ. Note continuity of Henle's sheath with the sheath of the muscle fibre; note also the distinction between the nuclei of Henle's sheath (*n.H.*) and of Schwann's sheath (neurolemma) (*n.n.*). The "perilemma" (*p.*) and sole-plate protoplasm are visible, but not its nuclei. *a.* axon; *m.* myelin sheath. Gold chloride; leg muscle.

Fig. 8. A more spreading type of end-organ. Gold chloride; leg muscle; microphotograph.

Fig. 9. Living motor end-organ from sartorius muscle, examined in physiological saline. In this specimen the axial substance of the axon end-ramification was partly visible. "Perilemma" not seen. Only a few sole-plate nuclei visible. Zeiss Apochr. 2 mm., oc. × 10.

Fig. 10. Degenerated coarse motor nerve, with the end-organ seen in profile. (From animal *G*; 146 days' degeneration.) Henle's sheath forms a cap (telolemmal sheath) over the Doyerean eminence, and becomes continuous with the sheath of the muscle fibre; the nerve fibre is represented only by its neurolemmal component (cord of Büngner), the multiplication of its nuclei being especially evident within the small nerve bundle from which the fibres emerge. Note continuity of cord of Büngner with "perilemma." Intercostal muscle; gold chloride.

Fig. 11. Ending of coarse motor nerve; drawn from a Bielschowsky preparation in which the "perilemma" (*p.*) has become visible. Usually only the fibrillar end-ramification stains by this method. Note the two types of nuclei of the end-organ: the rounded, deeply staining, telolemmal nuclei of Kühne (*t.n.*) and the pale oval sole-plate nuclei (*s.n.*). Note also the curious relation of the former to the end-ramification. The sole-plate nuclei definitely avoid the substance of the "perilemma". Two muscle nuclei (*m.n.*) are also seen. Tail muscle. Zeiss Apochr. 2 mm., oc. × 10.

Fig. 12. The same. This is a simple case and is drawn to show that the telolemmal nucleus may sometimes lose its apparent association with the axon end-ramification. Tail muscle; Bielschowsky preparation. Zeiss Apochr. 2 mm., oc. × 10.

Plate II

Fig. 13. Drawing of a motor nerve ending stained with methylene blue, in which the fibrillar and perifibrillar components of the axon terminal, and also the "perilemma" and sole-plate protoplasm were simultaneously visible. Only a few sole-plate nuclei are seen. Leg muscle. Zeiss Apochr. 2 mm., oc. × 10.

Fig. 14. Degenerated motor end-organ from animal *D* (102 days' degeneration); compare this with figs. 10, 11, 12. The end-ramification of the nerve has completely disappeared; the "perilemma" persists unaltered apparently; note connection of cord of Büngner with "perilemma." Leg muscle; Bielschowsky preparation.

Fig. 14*a*. Microphotograph of same.

Fig. 15*a*. Drawing of profile view of coarse medullated fibre ending on a muscle fibre. Note continuity of Henle's sheath with sheath of muscle fibre. For diagrammatic purposes two branches of the end-ramification have been drawn on to the same plane of focus. In figs. 15*b* and *c* the end-organ has been photographed with the lower of these branches in focus. Note also the fine filaments connecting the branches of the nerve with Krause's membrane of the muscle fibre. Two sole-plate and one telolemmal nuclei present. Tail muscle; Bielschowsky method.

Fig. 16. Four fibres ending on muscle fibre by numerous end-knobs "terminaison en grappes". Note connection of end-knobs with Krause's membrane. One of these end-knobs, the ninth from the left, with this connection exactly in focus, is shown in fig. 16*a* (microphotograph). Gold chloride.

Plate III

Fig. 17. Microphotograph of gold chloride preparation of leg muscle, showing multiple innervation of single muscle fibres. There are five muscle fibres in the bundle that traverses the photograph from top to bottom. The "en grappes" and "en plaque" endings are indicated respectively by *g* and *p*; also the number of the muscle fibres on which they occur. Each muscle fibre has at least one "plate" ending; in addition the number of "grape" endings, derived from finely medullated or unmedullated nerves, on muscle fibres 1–5 are 1, 2, 1, 1, 3 respectively. The minute ending indicated by *g*5 just below *p*5 is shown at greater magnification in fig. 19.

Fig. 18. A very delicate non-medullated fibre arises as a branch from a thicker (finely medullated?) fibre; it accompanies the latter and ends by a loop within the grape-like ending of the former. Bielschowsky preparation; leg muscle.

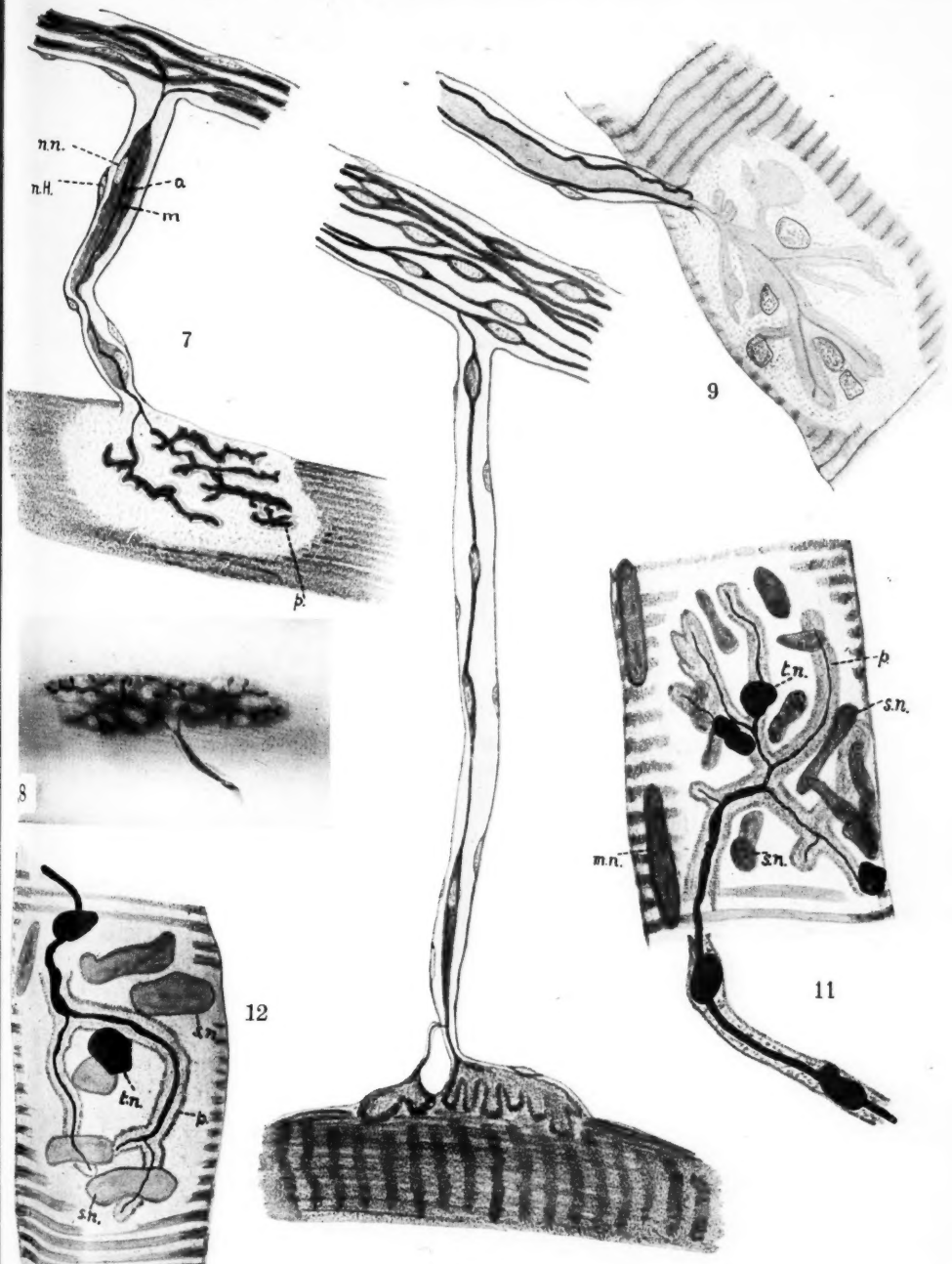
Fig. 19. Delicate non-medullated fibre forming a very simple end-organ. A small amount of granular sole-plate protoplasm is visible. This is the ending *g* 5 just below *p* 5 of fig. 17.

Fig. 20. A similar case, in which the hypolemmal position is evident. Gold chloride. Zeiss Apochr. 2 mm., oc. × 15.

Fig. 21. A simple type of neuromuscular spindle, showing the sensory nerve forming an end-organ on the muscle fibre. Gold chloride; tibialis anticus.

Fig. 22. Portion of neuromuscular spindle from animal *A*, in which the somatic motor nerves have degenerated 57 days. Sensory ending intact; extracapsular motor nerve degenerated. In figs. 21 and 22 note the continuity of the sheath of Henle of the sensory or motor fibres with the sheath of the spindle fibre. Gold chloride preparation.

Fig. 23 *a*, *b*, *c*. Three varieties of somatic motor nerve ending on the extracapsular region of the spindle fibre. 23 *a*. Weakly medullated fibre. 23 *b* and *c*. Unmedullated fibres terminating in end-knobs ("en grappes" type). The ending shown in fig. 22 will serve as an example of a form commonly met with, showing well-developed Henle's sheath. Gold chloride; tibialis anticus.



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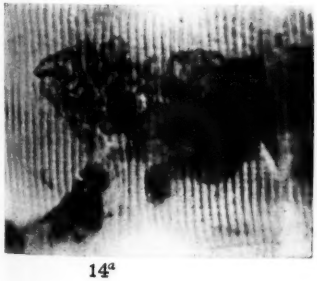
15c

15b



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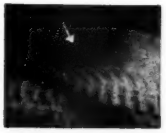

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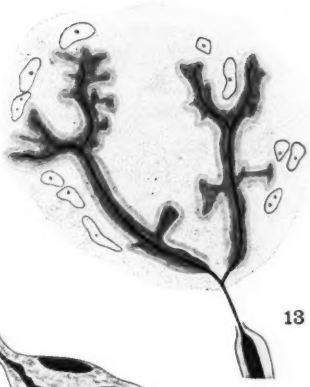

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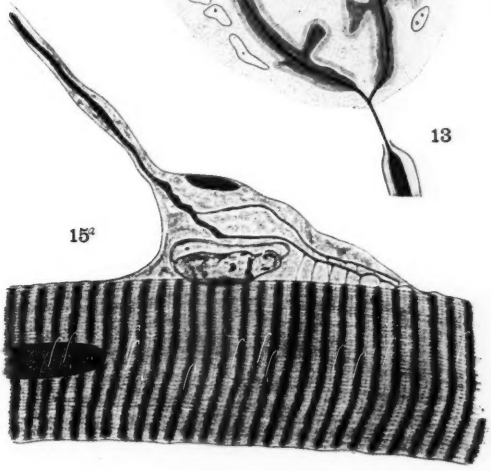

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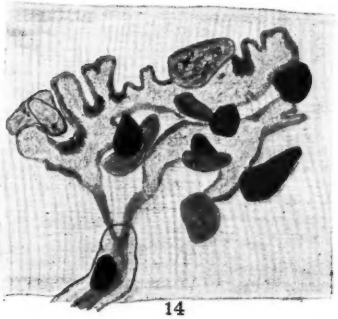

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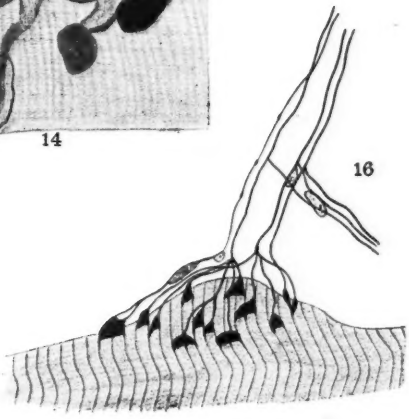

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THE ANATOMY OF THE INTERCOSTAL NERVES

By F. DAVIES, R. J. GLADSTONE and E. P. STIBBE

From King's College and the London Hospital Medical College

As long ago as 1916 Walmsley (1) drew attention to certain inaccuracies in the orthodox description of the intercostal nerves and muscles. In 1930, two of the present writers (2) again invited the attention of the Anatomical Society to this subject and stated that the intercostal nerves (and vessels) lie *deeply* to the internal intercostal muscles, and that their manner of branching and distribution is not in accord with the usual descriptions. The present paper is the result of investigations carried out independently in two departments, the data having been accumulated over a period of nearly a year before any comparison was made. These data comprise a large number of dissections of adult and still-born subjects, and the examination of serial transverse and longitudinal sections of young embryos. On comparing results, sufficient common ground was discovered to lead to the postulation of the following as the correct description of the anatomy of the intercostal nerves and muscles.

The intercostal nerve, two of its terminal branches, and the accompanying vessels lie deeply to the internal intercostal muscle in their whole extent. The conception that the intercostal nerve is embedded in the internal intercostal muscle is due to the fact that a muscular stratum lies deeply to the nerve. We agree, however, with Walmsley (1) in regarding this deep stratum not as an intrinsic part of the internal intercostal muscle but in recognising it as an independent "intracostal" muscle.

Before reaching the angle of the rib, the trunk of the intercostal nerve gives off a branch to the external intercostal muscle, and then divides into three main branches: an upper (anterior cutaneous) which occupies the subcostal groove and is the principal or main nerve for the greater extent of the intercostal space; a lower which runs for a varying distance along the upper border of the rib below, and which we call the collateral branch; and an intermediate, the lateral cutaneous branch. Usually each nerve has also a communication with the neighbouring intercostal nerve by a fine filament crossing the deep aspect of the rib. The above description applies also to the disposition and distribution of the nerves occupying the lower spaces. The arrangement in the abdominal wall is similar to that in the intercostal spaces, but the intercommunications are rather more complex.

Certain features of this description may now be discussed in detail.

(1) *Plane of the intercostal nerves.* The lateral cutaneous branch of each nerve has a short course between the internal and external intercostal muscles before finally piercing the latter. With this exception, *at no part of the intercostal space can any large nerve be found between the external and internal intercostal muscles* (fig. 1). In other words, *in no part of its course does the intercostal nerve trunk before division or its terminal continuation the anterior cutaneous nerve lie between the external and internal intercostal muscles.*

The intercostal nerve trunk and its two terminal cutaneous branches are separated from the pleura by two strata:

(*a*) A definite thin plane of muscle, whose fibres have the same direction as that of the internal intercostal muscle, which we regard as the intracostal muscle. The upper part of this immediately below the rib above the space is thin and membranous.

(*b*) An immediately extra-pleural stratum consisting of subcostal muscles posteriorly, transversus thoracis anteriorly, and between the two a fascial plane (the sternocostal fascia, Stibbe (3)).

Owing to the thin membranous nature of the internal covering (sternocostal fascia and upper membranous part of the intracostal muscle) the chief nerve trunks in the intercostal space are plainly visible on the inner aspect of the undissected thoracic wall (fig. 2). This is correctly represented by Henle (4), but in no other work accessible to the writers.

(2) *The muscles of the intercostal spaces* are four in number, namely from without inwards (fig. 3): external intercostal, internal intercostal, intracostal, subcostal. The upper attachment of the internal intercostal is not to the inner lip, but into the *floor* of the subcostal groove (figs. 3 and 4). Its fibres spread out to form a sort of carpet lining the groove, and on the deep aspect of this lies the nerve. This appearance is well seen in the embryo (figs. 4 A, B, C) where the distinction between external and internal intercostals is less striking than that between the internal intercostal and the intracostal.

The intracostal muscle is approximately co-extensive with the internal intercostal fibres, but becomes more membranous in its anterior part. Muscular below, its fibres end above in a thin membranous sheet which is attached to the inner (upper) lip of the subcostal groove (fig. 3), and through which the nerve can be seen as above described.

(3) *Branching of the intercostal nerve.* We find that the conception of a single nerve running the length of the space is incorrect. At any part of the intercostal space anterior to the angle of the rib two nerves will be found, the main nerve (anterior cutaneous) above, and the collateral branch below; while, between the angle of the rib and the mid-axillary line are three nerves (fig. 3), the additional nerve (incidentally the largest of the three) being the lateral cutaneous. The orthodox description should accordingly be modified as shown in figs. 1 and 2. The fibres of the collateral branch constitute an additional anterior cutaneous supply. Commonly the collateral joins the main (anterior

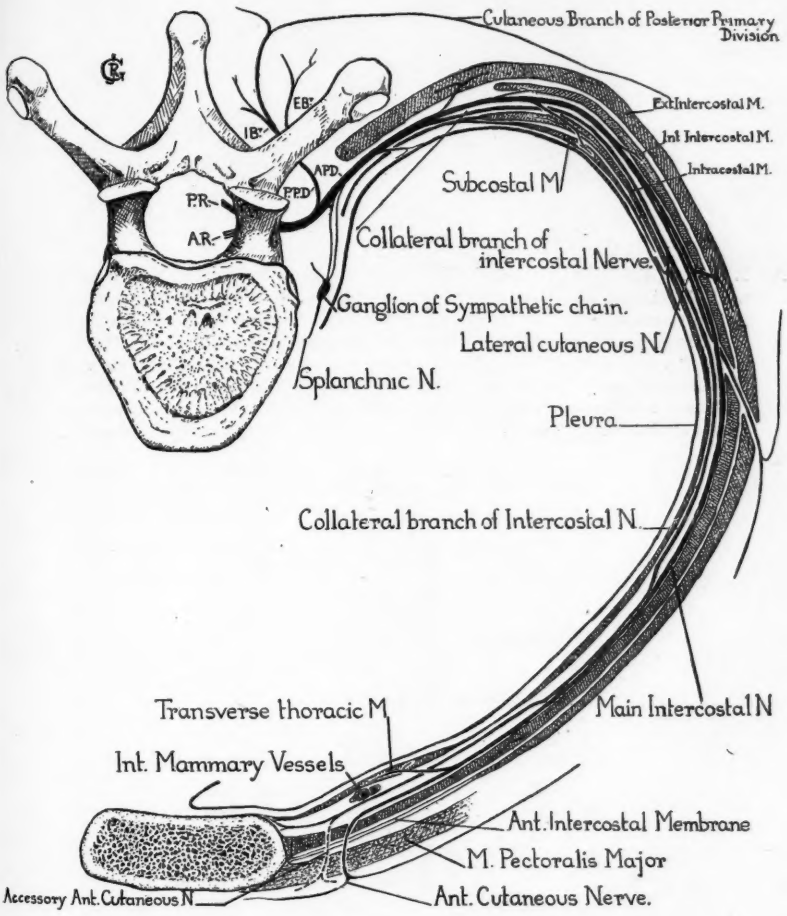

Fig. 1. Diagrammatic representation of a horizontal section through an upper intercostal space. The scheme shows the position of the intercostal nerve and its main branches between the intracostal muscle and the internal intercostal muscle. It also shows the division of the main nerve into three principal branches: (1) the main anterior cutaneous nerve, above; (2) the lateral cutaneous nerve, intermediate; (3) the collateral branch, below. It will be observed that the collateral branch rejoins the main anterior cutaneous nerve in the anterior part of the space. After coursing forward with this for a variable distance it frequently leaves it, and may pierce the internal intercostal muscle, anterior intercostal membrane and greater pectoral muscle to terminate as an accessory anterior cutaneous nerve. In addition to the nerves indicated in the diagram, communicating branches are frequently present which join the intercostal nerve above or below the nerve of any given space.

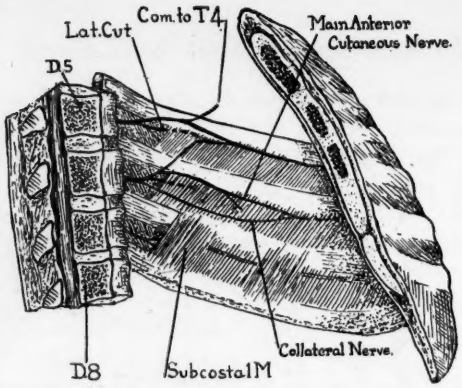

Fig. 2. From a dissection by Dr E. P. Stibbe. The fifth, sixth and seventh intercostal spaces of a full-time human foetus. In the fifth and sixth spaces the subcostal and intracostal muscles have been removed so as to expose the intercostal nerves lying upon the insertion of the internal intercostal muscle into the floor of the subcostal groove. The sixth intercostal nerve gives off a large communicating branch to the fifth nerve. In the seventh intercostal space the subcostal and intracostal muscles have been left in position, and the main anterior cutaneous branch of the intercostal nerve is just visible through the thin membranous insertion of the internal intercostal muscle into the upper border of the subcostal groove.

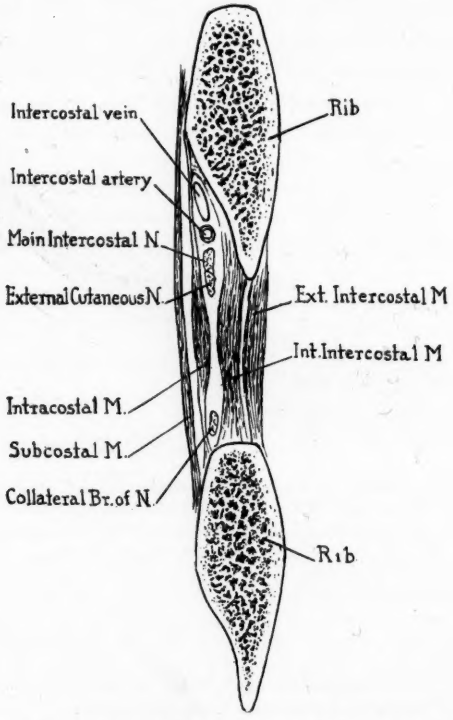

Fig. 3. Diagram of a vertical section through an intercostal space, showing the relationship of the vessels and nerves to the muscular layers.

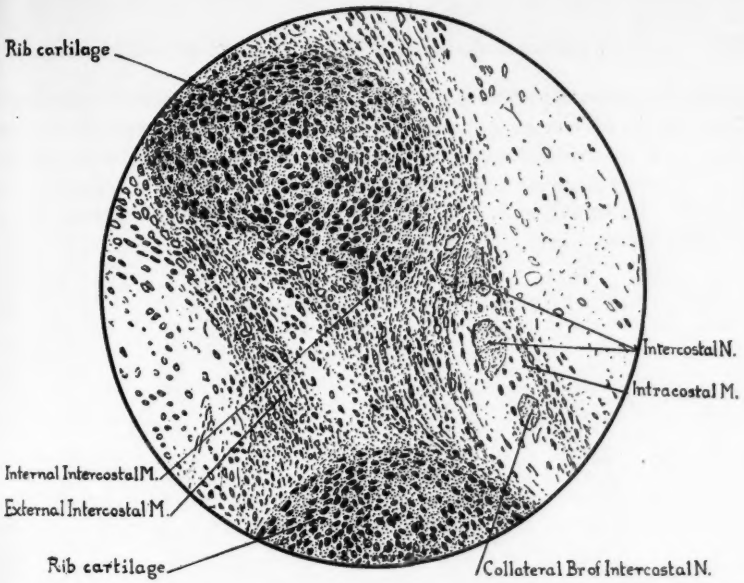

Fig. 4 A. Sagittal section through the fourth intercostal space of a human embryo 12 mm. in length, showing the main intercostal nerve and its collateral branch situated between the extrapleural stratum of muscle and the internal intercostal muscle.

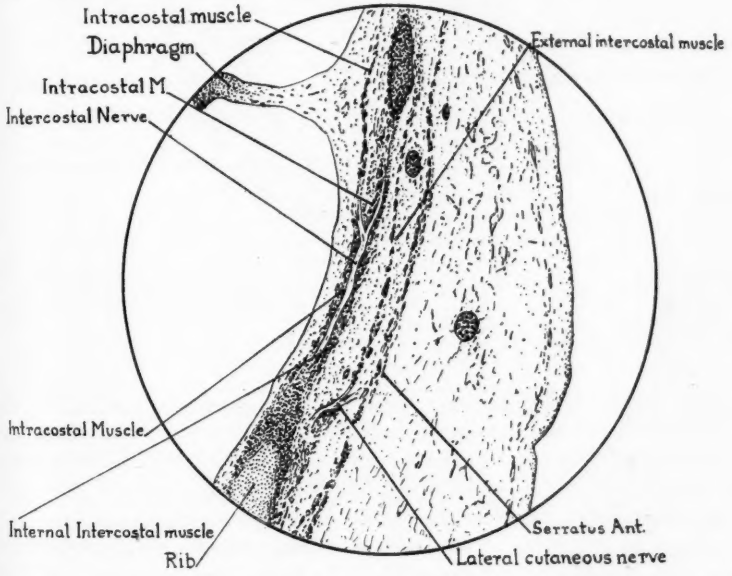

Fig. 4 B. Section passing obliquely through an intercostal space in the mid-thoracic region of a 20 mm. human embryo showing five muscular strata, which from within outwards are: 1, subcostal; 2, intracostal; 3, internal intercostal; 4, external intercostal; 5, serratus anterior. The main intercostal nerve lies between the intracostal muscle and the internal intercostal muscle.

cutaneous) nerve anywhere between the mid-axillary line and the anterior end of the rib, in which case it finally leaves the nerve to be distributed as a lower additional anterior cutaneous nerve. There are thus two anterior cutaneous nerves in each intercostal space, just as there are two in each "segment" in the anterior abdominal wall. Not infrequently the collateral branch remains independent throughout its course.

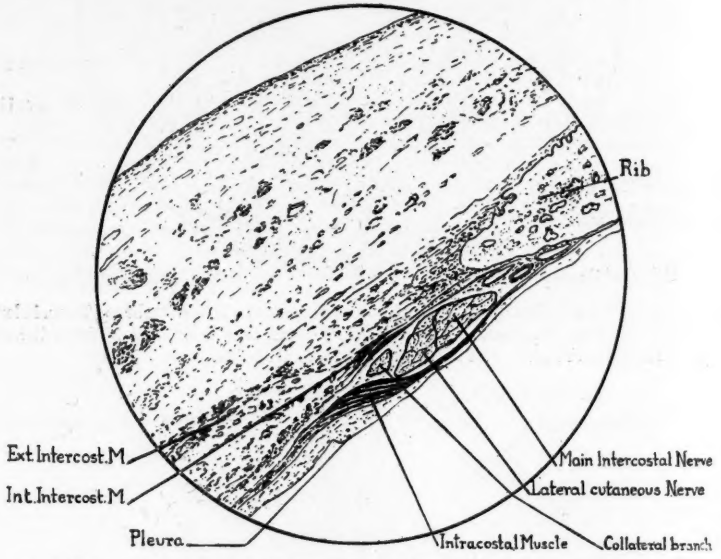

Fig. 4C. Oblique section through the upper part of an intercostal space of a 4·5 cm. human embryo, showing the intercostal vessels and nerves lying in the space between the intracostal muscle and the internal intercostal muscle. The subdivision of the intercostal nerve into three branches is clearly visible, namely: (1) main anterior cutaneous branch of the intercostal nerve lying above; (2) lateral cutaneous nerve intermediate and at this part of its course bound up in the same sheath as the main nerve; (3) collateral branch, below and separated by a short distance from the lateral cutaneous nerve.

The lateral cutaneous nerve remains in the deep plane with the other branches until it has nearly reached the level of its exit from the space, where it pierces the internal and external intercostal muscles obliquely. The course of this nerve between the two intercostal muscles is thus very short (fig. 1).

(4) *Course of the lower six intercostals.* Each of these commonly pierces the diaphragm as a single trunk, the collateral branch having already rejoined the main (anterior cutaneous) nerve (fig. 5). Sometimes, however, two nerve trunks (main and collateral) pierce the diaphragm and join in the anterior abdominal wall (fig. 6). Between the transversalis and internal oblique muscles there is a very free plexus formation (figs. 5, 6, 7). By "stripping" the

nerves backwards from the lateral border of the rectus it can be shown that any one nerve in this region contains fibres from at least two, and sometimes three,

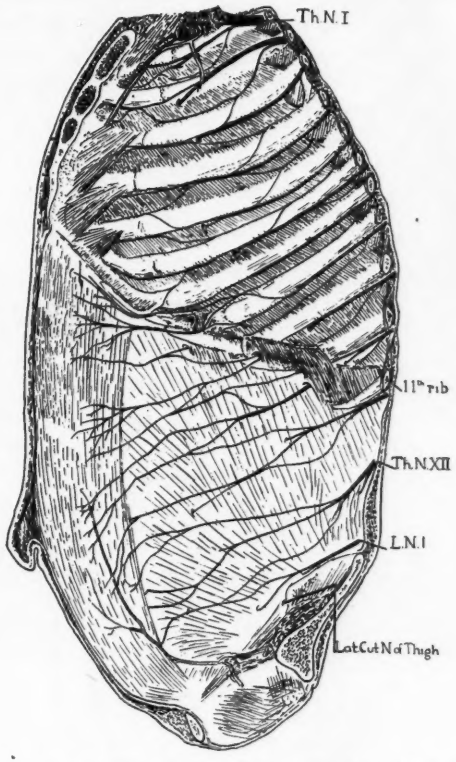

Fig. 5. From the dissection of a human foetus by Dr F. Davies. The pleura, subcostal, intracostal and transverse abdominal muscles have been removed, and the thoracic and abdominal muscles exposed from the inner side. A typical intercostal nerve is seen to divide into three main branches: (1) an upper which terminates as the principal anterior cutaneous nerve; (2) an intermediate branch which is bound up in the same sheath with the main branch for a variable distance before leaving it to become the lateral cutaneous nerve; (3) and a collateral branch which is given off in the posterior part of the space and then courses along the lower part of the space for a considerable distance. It may then rejoin the main nerve and finally terminate with it as the anterior cutaneous nerve, or it may again separate from the principal nerve and terminate as an accessory cutaneous nerve. Communicating branches are seen crossing the inner surfaces of the ribs. The same subdivision of the main nerve into three principal branches and communications with adjoining intercostal nerves is seen in the abdominal wall as that which takes place in the thoracic wall.

intercostal nerves. Moreover, any one nerve at the lateral border of the rectus is distributed to two segments of the muscle. It is certain, therefore, that the rectus segments do not receive a "segmental" nerve supply, but that each

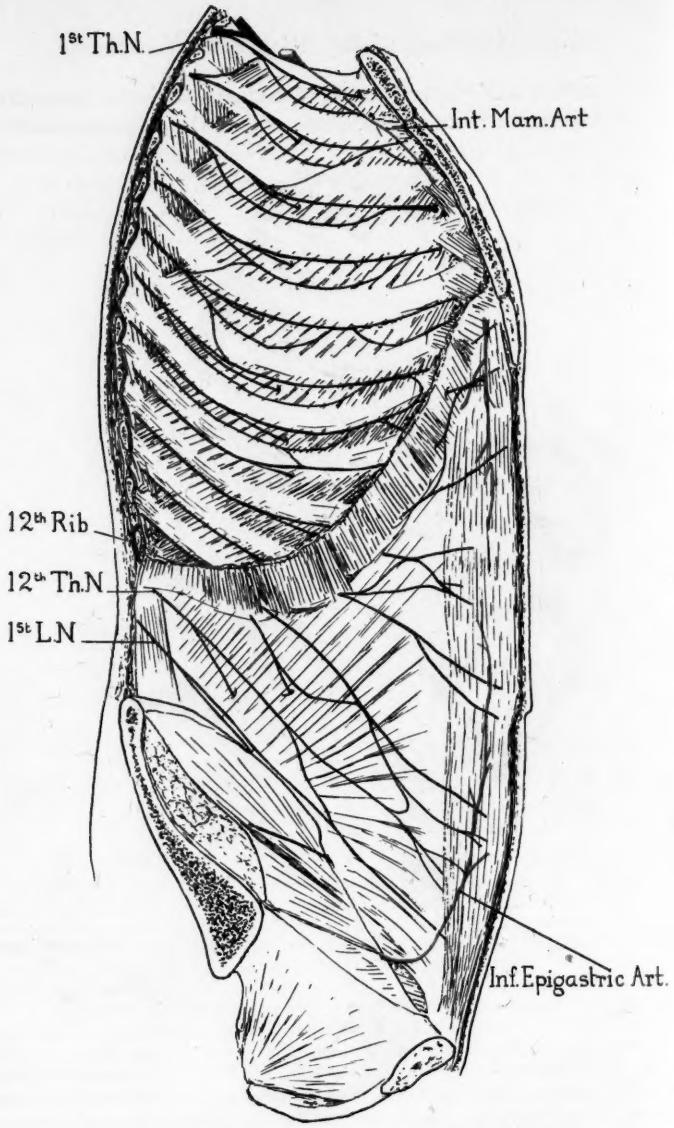

Fig. 6. Diagram of the distribution of the intercostal nerves founded on dissections made by Dr E. P. Stibbe. The figure represents the left side of an adult human subject seen from the inside. The pleura, peritoneum, subcostal, intracostal and transversus abdominis muscles have been removed, and the thoracic and first lumbar nerves exposed, lying on the inner aspect of the internal intercostal and internal oblique muscles. The division of the main nerve into three principal branches is shown, and also the communications between the intercostal nerve of one segment and the nerve above or below it in the series. No communication however was found between the tenth and the eleventh thoracic nerves. The relation of the nerves to the superior and inferior epigastric arteries is also indicated.

segment is supplied by three "segmental" nerves at least. The twelfth thoracic nerve communicates freely with the ilio-hypogastric.

(5) *Distribution to the diaphragm.* Each of the intercostal nerves from the seventh downwards gives a twig to the diaphragm; this may be derived from the collateral branch or from the "main" nerve, or there may be two branches, one from each division. The branch from the seventh is usually single, large, and given off from the single trunk of reunion of collateral and "main" divisions. Kiss and Ballon(5) conclude that these branches are sensory, though Felix(6) attributes motor function to the branch from the twelfth intercostal. The results of clinical avulsion of the phrenic nerve seem to show that it is the only motor supply of the diaphragm.

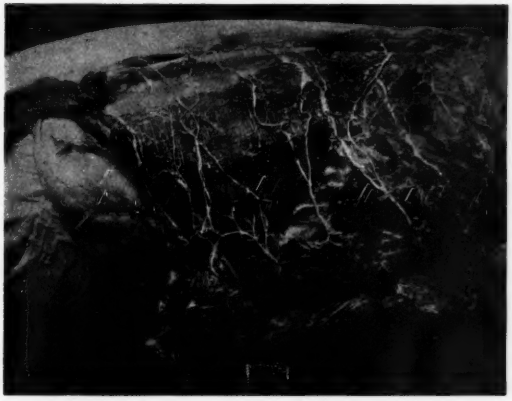

Fig. 7. Photograph of a dissection by Dr E. P. Stibbe, to show plexus formation of intercostal nerves in anterior abdominal wall.

(6) *Distribution in rectus muscle and overlying skin* (fig. 8). At the lateral border of the rectus muscle, each nerve divides into two branches, an upper and a lower; the lower branch represents the collateral branch (cf. anterior ends of intercostal spaces).

The upper or "chief" nerve enters the back of the muscle in the region of the tendinous intersection and near the lateral border of the muscle. It courses inwards for a short distance and divides into three sets of branches: one to the muscle segment above, one to the muscle segment below, and an anterior cutaneous. The latter enters the skin near the linea semilunaris, and is a member of the lateral series of anterior cutaneous nerves.

The lower or collateral branch enters the muscle below the corresponding tendinous intersection, courses inwards, communicates with the upper branch, and ends as the medial anterior cutaneous branch usually just below the linea transversa and just outside the linea alba.

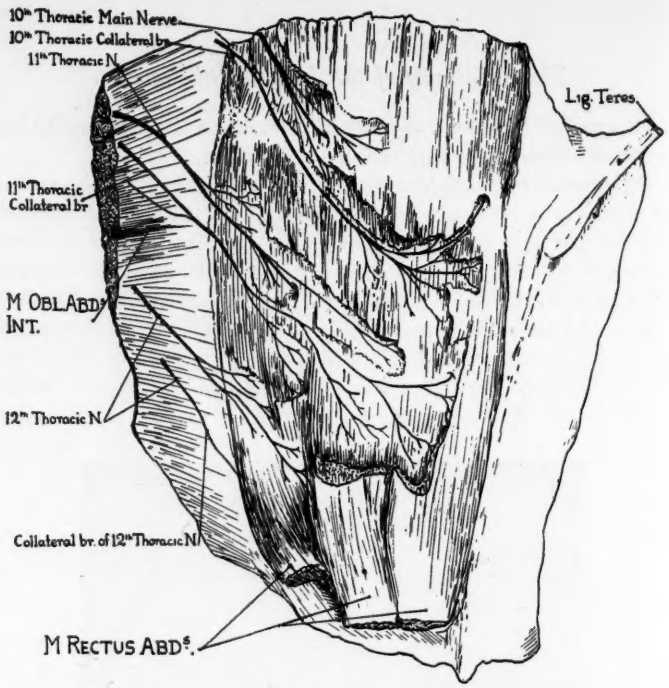

Fig. 8. From a dissection by Dr F. Davies. A portion of the abdominal wall is viewed from behind. The transversus abdominis muscle and the posterior wall of the sheath of the rectus abdominis muscle have been removed. The terminal distribution of the tenth, eleventh and twelfth thoracic nerves is seen to consist of an upper and lower branch. The upper branch, after having given off muscular branches to the rectus muscle, ends as the lateral anterior cutaneous branch. The lower branch gives off branches to the muscle and finally terminates as the medial anterior cutaneous branch. The drawing also indicates the relationship of the nerve fibrils to the lineae transversae and the superficial, intermediate and deep strata of the rectus muscle.

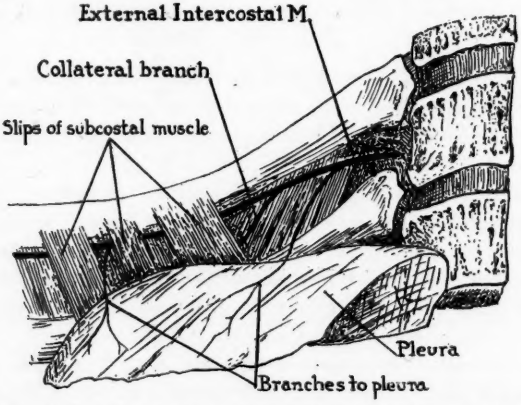

Fig. 9. From a dissection by Dr E. P. Stibbe. The vertebral end of a lower right intercostal space viewed from the front. The pleura has been turned down and the posterior intercostal membrane removed. The main intercostal is seen to give off a collateral branch and branches to the pleura.

The twelfth thoracic nerve passes entirely in front of the rectus muscle; the upper branch ends in skin, the lower is distributed to the Pyramidalis muscle and the skin.

SUMMARY

1. The muscles of the chest wall are four in number in each space: external intercostal, internal intercostal, intracostal and subcostal from without inwards. The subcostal muscle is variable in its extent, the others constant in each space.

2. The intercostal nerves and vessels are confined to the plane between the internal intercostal and intracostal muscles.

3. Each intercostal nerve divides at the back of the space into a series of branches:

(*a*) The "main" nerve, is prolonged as the anterior cutaneous branch.

(*b*) The lateral cutaneous.

(*c*) The collateral branch, either rejoins the anterior cutaneous branch nerve, or ends independently as a second anterior cutaneous branch.

4. The lower intercostal nerves form an elaborate plexus in the abdominal wall. Each muscle and skin "segment" receives branches from at least two and more commonly three spinal nerves.

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CERVICAL RIBS AND RUDIMENTARY FIRST THORACIC RIBS CONSIDERED FROM THE CLINICAL AND ETIOLOGICAL STANDPOINTS

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A large number of cases of 7th cervical and rudimentary 1st thoracic ribs have now been recorded, but there is much yet to be learned about these abnormalities. The relations of these abnormal ribs to the vertebral column and sternum, and to the principal nerve trunks, vessels and muscles have been minutely described by various authors, partly from the surgical, and partly from the morphological aspect. From the surgical standpoint, with regard to the relief of pressure symptoms by the removal of a part of the rib, or the division of the fibrous or muscular structures attached to it; and by anatomists with reference to the meaning of these variations considered from the morphological standpoint.

The true cause of these variations in the number, size and position of the ribs, and of their varying relations to the vertebral column and sternum, does not appear to have been discovered, although several well-known theories have been advanced in the attempt to find a solution of this difficult problem. Some of these theories are conflicting in nature, or inconsistent with ascertained facts; but as yet, nobody has either definitely confirmed or refuted certain of the particular points at issue. For instance: Do these variations indicate a general tendency towards decrease or increase in the number of ribs in the human race? or have they no phylogenetic significance? Are these variations germinal in origin? or are they due to some disturbance of the normal segmentation in early embryonic development? Are cervical ribs and additional vertebrae to be regarded as an exuberance of development, and rudimentary ribs or diminution of the number of ribs and total number of vertebrae, as defects of development? or is there a common cause for both types of variation? Is Ruges' theory of the formation of the right and left sternal bars by fusion of the ventral ends of the cartilaginous anterior thoracic ribs correct? or are the mesodermal bars which precede the development of the cartilaginous sternum evolved independently of the ribs in a mass of condensed mesodermal tissue, which arises medially between the rudiments of the shoulder girdle, and extends backwards in the form of two mesenchymal bars? This theory was propounded by Melville Paterson, and subsequently reaffirmed by other workers; for instance, Whitehead and Waddell, who hold that the bars arise *in situ* and join the median rudiment secondarily, and Hanson who believes that the sternum is an homologous structure throughout all groups of verte-

brate animals, that the anterior elements of the sternal apparatus arise in common with the shoulder girdle in intimate relation with the coracoids, and that the sternal bars, although they may be associated with the ribs secondarily, do not arise from these. This question we intend to deal with in a subsequent communication on the development of the sternum. It may be advisable, however, to state here that the evidence, both of ontogeny and of comparative anatomy, appears to support the latter view, the sternum primarily having been evolved in certain fishes and tailless Amphibia, as a support for the shoulder girdle, as a firm site of origin for the pectoral muscles and quite independently of the ribs. In *Rana* the ribs are short; they do not reach the sternum, and have no respiratory function; yet in the frog, the sternal apparatus is a well-developed structure consisting of an "episternal process," connected by fused epicoracoid cartilages with the sternum proper and the metasternum. It is, moreover, joined on each side by a well-developed clavicle and coracoid. The various conflicting theories which have been put forward by such authorities as Eisler, Rosenberg, Bateson or Weidersheim are well known. The last of these authors, it may be recalled, regarded the occurrence of cervical ribs in Man as an "atavism," and rudimentary 1st thoracic ribs as a "progressive variation," while others considered that the variations in the number of the costal elements and their relations to the vertebrae are simply "variations about a mean," which take place in the transitional regions of the vertebral column, and have no evolutionary importance.

It is not our purpose here to enter generally into the difficult question of meristic variations; we wish, however, to draw attention to a factor which appears to have an important bearing on the cases with which we are dealing. In a large proportion of the reported cases of cervical ribs and rudimentary 1st thoracic ribs, other anomalies have been present in the same subject. These are undoubtedly defects of development which have occurred at an early stage of embryonic life, and cannot thus be regarded as germinal variations having a phylogenetic significance. These defects of development are not limited to the skeletal system, but involve other systems such as the nervous and vascular. Some of these defects are primary in nature, and appear to be due to a disturbance of the normal process of segmentation; others are secondary and are produced as a direct result of the primary defect, e.g. complete absence, imperfect development, or atrophy of muscles owing to pressure on nerves; or are compensatory changes, e.g. the development of an adventitious joint in an unusual situation to compensate for absence of cleavage, or fusion of segments which normally articulate with each other by movable joints, figs. 1 and 2. They include such defects as congenital scoliosis of the vertebral column; synostosis and imperfect development of vertebrae; fusion of the atlas vertebra with the occipital bone; irregularity and asymmetry in the development of the base of the skull; anencephalus, spina bifida and syringomyelia; imperfect development of the clavicles; suppression of half or the whole of one or more vertebrae. Should the suppression of half a vertebra

occur in the thoracic region, there may be absence of the corresponding rib and intercostal structures on the same side. This condition may be associated with congenital dilatation of the colon. Various defects of the vascular system may also be present, such as supernumerary renal arteries accompanying a low position of one of the kidneys, or, in one case, a left-sided post-renal vena cava, associated with other anomalies of the veins, and of the nerve plexuses.

Fig. 1.

Fig. 2.

Fig. 1. Anterior aspect of the cervical and upper three thoracic vertebrae of case VIII, showing the fusion of the 2nd, 3rd, 4th and 5th cervical vertebrae, and 6th, 7th and 1st thoracic vertebrae. A pseudo-arthrosis can be seen between the body of the 5th cervical vertebra and the left half of its neural arch.

Fig. 2. Posterior view of case VIII, showing the fusion of laminae and articular processes of certain of the cervical vertebrae and secondary enlargement of the mastoid foramina.

DESCRIPTION OF CASES

Case I. Freda S., aged 1 year, was sent to hospital in 1930, because her back was bent. On examination, it was seen that the child was suffering from marked scoliosis with the summit of the convexity opposite the 9th dorsal spine. The deformity could not be corrected. Skiagrams show (fig. 3) a half vertebra in the region of the 9th thoracic vertebra on the left side. There are twelve ribs on the side of the half vertebra, and eleven only on the other.

The child was quite healthy in every other respect, and had no other congenital defects. There is no evidence of congenital deformities in the parents or their relations.

Case II. Monica T., aged 5 years and 8 months, came under observation at the age of 3, because of marked lateral curvature of the spine. She was treated

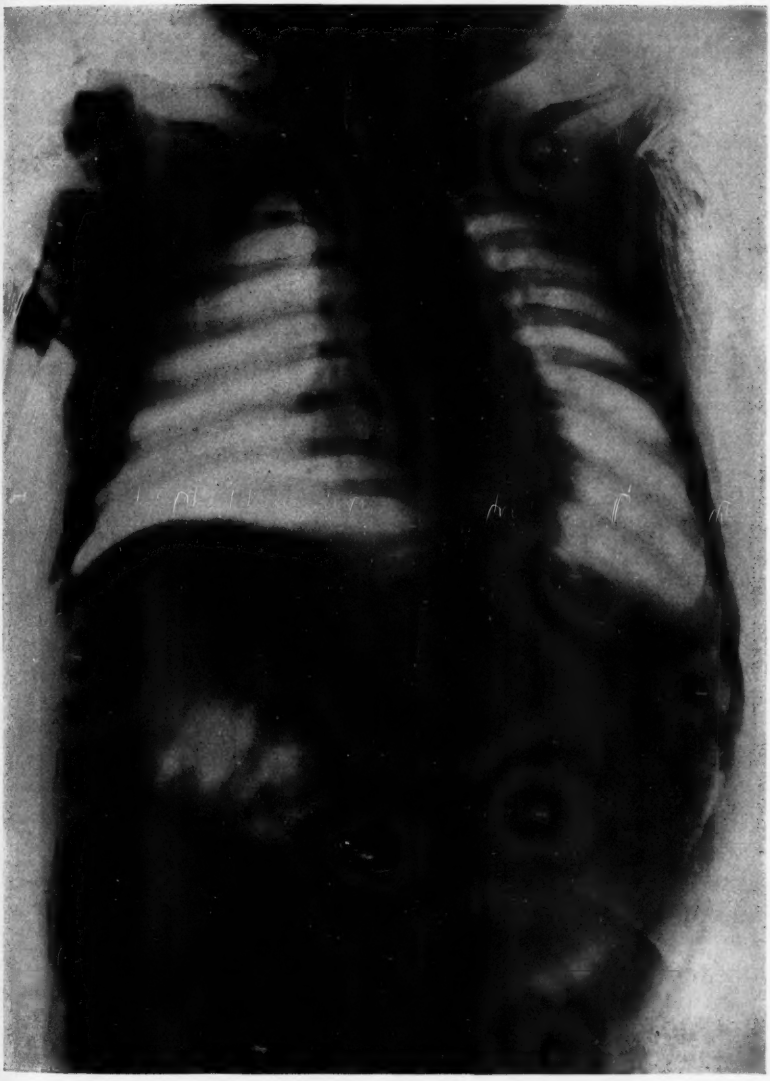

Fig. 3. Skiagram of case I, showing half vertebra in the region of the 9th thoracic vertebra, producing a scoliosis.

with a light spinal jacket. On examination, there were found severe scoliosis in the lower thoracic region, and a spina bifida occulta in the region of the 5th and 6th dorsal vertebrae. A skiagram (fig. 4) revealed half vertebrae in the region of the 2nd and 10th dorsal vertebrae. The 11th dorsal vertebra was in two parts. There was extensive malformation in the upper right ribs. The 2nd rib was absent and the 3rd bifid.

Case III. Case of bilateral cervical rib in a man aged 32, who came to hospital because of pain in the right hand, and some loss of power in the grip. He was a clerk by profession, and he noticed the pain in the hand was worse after playing tennis. On examination, the intrinsic muscles of the right hand were found to be wasted, and not so well developed as those in the left hand. The subclavian arteries could be seen pulsating in the supraclavicular fossae. On palpation, a cervical rib could easily be felt in each supraclavicular fossa. Skiagrams (fig. 5) confirmed the presence of bilateral cervical ribs, the one on the right side being more distinct. An X-ray photograph of the whole spinal column did not reveal any other abnormality. There were twelve pairs of thoracic ribs on each side.

An operation was performed in May 1922, and the right cervical rib was removed. It consisted of an osseous posterior two-thirds, and a fibrous anterior third, which was attached to the 1st thoracic rib. Recovery from symptoms was slow, and it was 6 months after the operation before all pain had disappeared, and the intrinsic muscles of the hand were equal to those on the left side. The patient has been kept under observation, has remained perfectly well, and, so far, no symptoms have been produced by the cervical rib on the left side.

Case IV. The case is somewhat similar to case III, in that bilateral cervical ribs were present, but symptoms were present on the right side only. The patient was a farmer, aged 23, who had complained of pain in the right hand for some months prior to coming under observation. On examination, there were definite wasting of the interossei muscles, and a weakness in the grip. No palpable cervical rib could be felt in the neck, but the subclavian artery appeared rather higher in the neck than normal. Skiagrams (fig. 6) revealed bilateral cervical ribs, the right one being the more conspicuous. The rest of the spinal column was normal as far as X-ray examination was concerned, there being twelve pairs of thoracic ribs on each side.

An operation was performed in December 1923, and the cervical rib was removed on the right side. The anterior half was fibrous, and pressed on the lowest brachial nerve cord. Recovery was uneventful, but it was nearly 6 months after the operation that the atrophied muscles in the hand had regained their normal tone, in spite of massage treatment. When seen 7 years after his operation, he was in good health, with no symptoms whatever. The left cervical rib had never given rise to any symptoms.

Case V. Mrs H. A., aged 21, was sent to hospital, because her left hand was becoming weaker, and she found it difficult to do her household duties, espe-

Fig. 4. Skiagram of case II, showing half vertebrae in the region of the 2nd and 10th dorsal vertebrae.

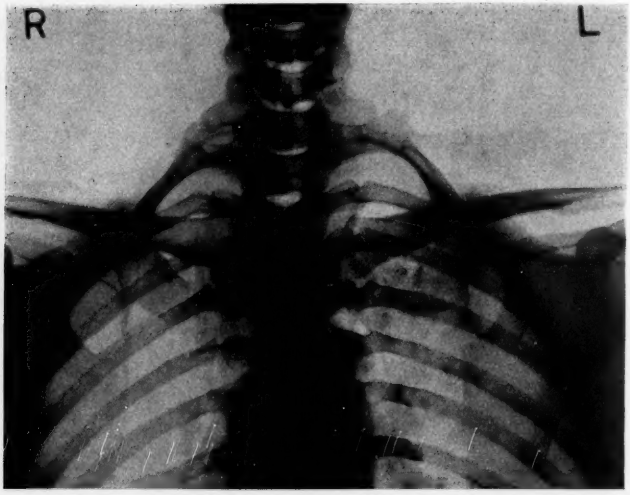

Fig. 5. Skiagram of case III, showing bilateral cervical ribs.

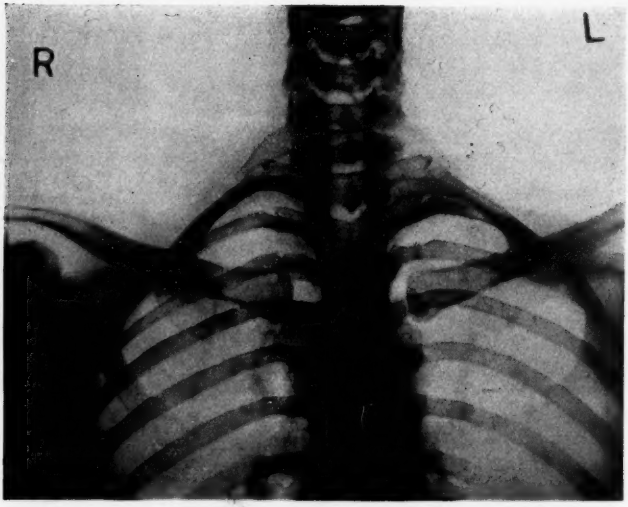

Fig. 6. Skiagram of case IV, showing bilateral cervical ribs.

cially ironing. On examination, there was distinct wasting of the interossei muscles, and definite loss of grip on the left side. No palpable tumour could be felt on either side of the neck. X-ray examination revealed a cervical rib on each side (fig. 7), that on the left being the larger. Complete X-ray examination of the spine did not demonstrate any other abnormality. There were twelve pairs of thoracic ribs on each side.

Operation for removal of the left cervical rib was carried out in March 1924. The anterior part of the rib was quite fibrous, while the posterior portion was

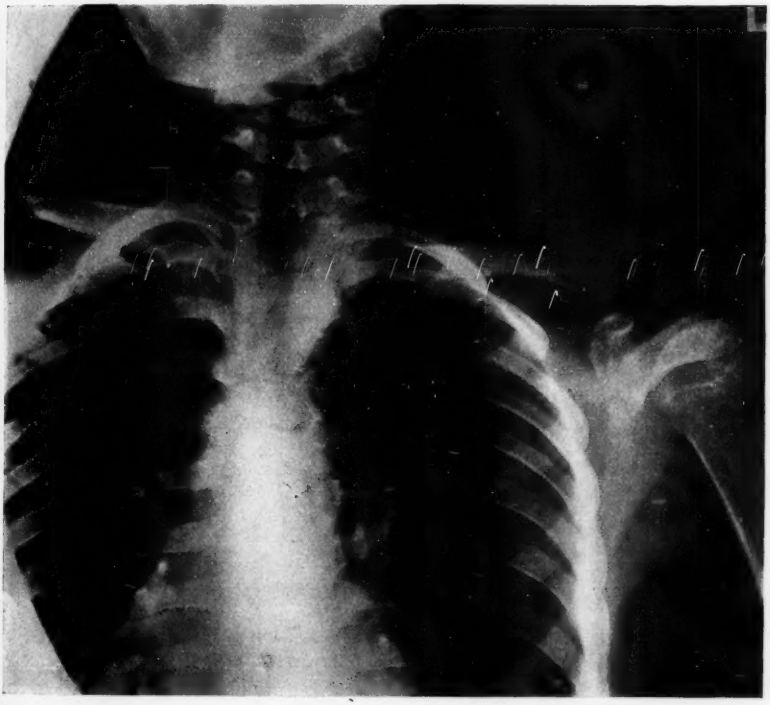

Fig. 7. Skiagram of case V, showing bilateral cervical ribs, that on the left side producing symptoms.

osseous. The patient made a good recovery, and was able to do any kind of work some 4 months after her operation. When seen 4 years afterwards, she was still in good health, and did not complain of any symptoms. In this case again, although a cervical rib was present on the right side, it did not produce any symptoms.

Case VI. This case was a man aged 24, who came to hospital complaining of pain and weakness in his right hand and arm. On examination, a very

definite cervical rib could be palpated in the right supraclavicular fossa. Skiagrams (fig. 8) revealed a very definite cervical rib, which articulated anteriorly with the 1st thoracic rib. No cervical rib was present on the left side. By X-ray examination of the whole spine, twelve pairs of thoracic ribs were seen. The cervical rib was excised in June 1925, and the patient made a complete recovery, and was able to go back to his work as a carpenter. When seen 2 years later, he was doing full work and suffering no disability.

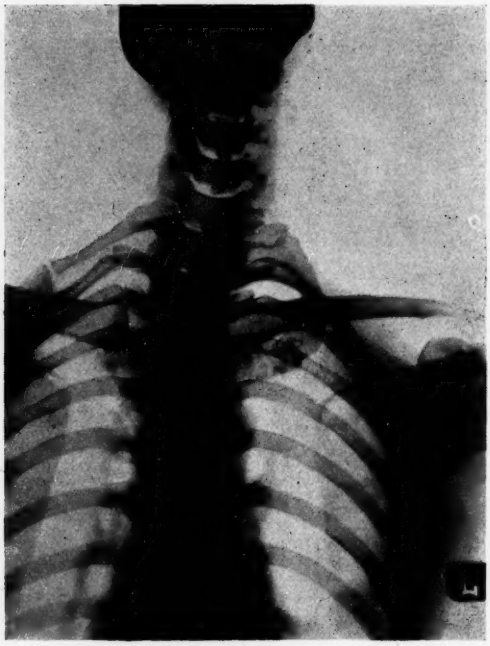

Fig. 8. Skiagram of case VI, showing cervical rib on the right side which articulated with the 1st thoracic rib.

Case VII. This case is of interest, because the body of the sternum was cleft, the ribs on each side articulating anteriorly in a sternal bar. The manubrium sterni is quite normal, and the 1st and 2nd ribs on each side articulate with it.

The child, whose present age is ten years, has been under observation since infancy, because of her chest. The photograph (fig. 9) shows the deep cleft between the anterior ends of the ribs on each side.

Case VIII. Rudimentary 1st thoracic ribs, discovered in a dissecting-room subject. The principal features of the skeleton were: a pair of rudimentary 1st thoracic ribs, each joined by a fibrous band to the pointed outer end of the 1st

costal cartilage. This articulated by its base with the lateral border of the manubrium just below the sternoclavicular joint, in the usual situation of the 1st rib cartilage; twenty-five presacral vertebrae; vertebral formula—C. 7, Th. 13, L. 5, S. 5, Co. ? 4. Thirteen pairs of ribs, including the rudimentary 1st pair; scoliosis of the vertebral column associated with irregularity and ankylosis of certain of the cervical vertebrae. The occipital bone was misshapen and asymmetrical.

Fig. 9. Photograph of case VII, showing deformity of chest.

The subject was an adult male, who was certified to have died from bronchitis and tuberculous disease of the vertebral column. On enquiry into the history of his illness it was ascertained that no symptoms were complained of which would indicate injurious pressure by the abnormal ribs on either nerve cords or vessels. The head and upper part of the cervical segment of the vertebral column were inclined to the left, there being a curve with the convexity to the right at the junction of the neck with the thorax. Below this level the bodies of the vertebrae inclined to the left, the axis of the column returning to the median plane, and a compensatory bend being present in the lower thoracic region with the convexity to the left. Owing to the deformity of the vertebral column and ribs, the heart was displaced to the right, its apex lying behind the

body of the sternum, while the whole of the right lung was compressed between the thoracic wall laterally, and the vertebral column and mediastinal structures medially. The right pleural cavity contained a considerable quantity of inspissated pus. The ductus arteriosus was incompletely obliterated, there being a narrow channel which just admitted a small bristle. The endothelium lining the vestibule of the left auricle was roughened by calcareous deposits.

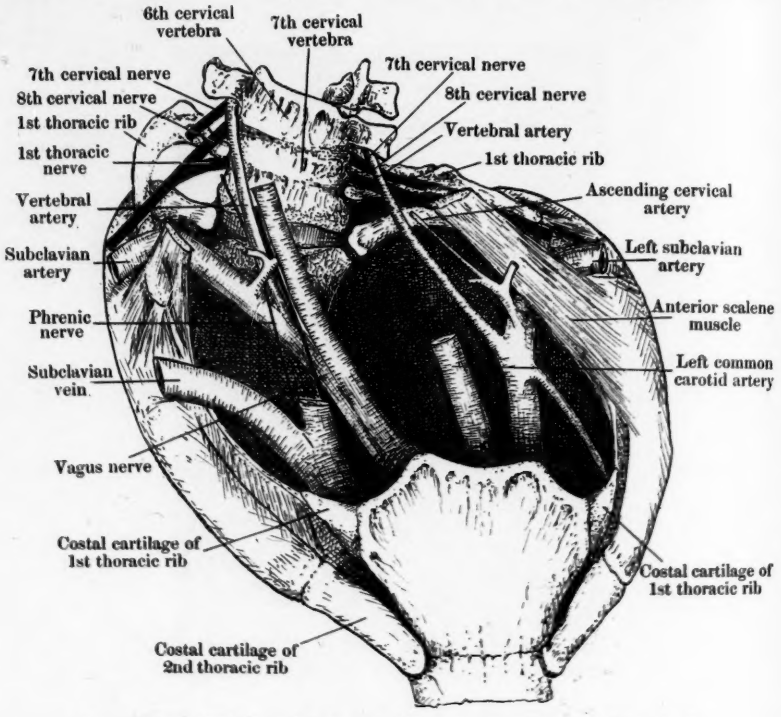

Fig. 10. Case VIII. Drawing showing bilateral rudimentary 1st thoracic rib.

The spleen was much enlarged. The left kidney was considerably lower than normal, and two accessory renal arteries entered its upper pole.

The rudimentary 1st rib of the right side, fig. 10, articulated with the body and transverse process of the 8th vertebra (presumably the 1st thoracic vertebra). The rib was so highly curved that its chord, measured from head to tip, was 4·2 cm., while the measurement along its convex border was 8 cm. The shaft of the rib ended in a blunt process which was connected by a fibrous band with the 2nd thoracic rib, and the tip of the 1st costal cartilage. This cartilage was triangular in shape, its base being attached to the lateral angle of the manubrium in the usual situation of the 1st rib cartilage, and its apex continuous with the fibrous cord. The inner border of the rib at the junction of the

neck with the shaft and the adjacent part of the upper surface of the shaft was rough for the attachment of the scalenus medius muscle. Owing to the curve of the upper cervical vertebrae to the left, the right vertebral artery as it coursed up to the foramen in the transverse process of the 6th cervical vertebra lay just medial to the head of the rudimentary rib, and the right phrenic nerve, which was also deflected medially, crossed in front of the neck of the rib. The subclavian artery on the right side crossed the shaft of the 1st thoracic rib in front of the scalenus medius muscle, and the lower primary trunk of the brachial plexus. The artery lay behind the attachment of the anterior scalene muscle to the tip of the rib and the fibrous band which was prolonged forward from this to the 1st costal cartilage. The subclavian vein crossed the fibrous band and 2nd rib in front of the scalenus anterior, and beyond the tip of the 1st rib. Some of the superficial fibres of both the scalenus anterior and the scalenus medius muscles passed over the 1st rib and gained attachment to the 2nd rib. Fibres representing the external and internal intercostal muscles also passed between the 1st rib with its fibrous prolongation and the 2nd rib.

The 2nd right rib was long and placed very obliquely. It had the usual characters of a 2nd thoracic rib, and its cartilage joined the sternum at the junction of the manubrium with the body. The cartilage did not, however, pass horizontally inward to join the sternum, but approached the joint obliquely, turning downward from the thoracic inlet to the sternal angle, fig. 10. The 2nd rib thus appears to have been displaced upwards to compensate for the rudimentary condition of the 1st rib. The chord of the 2nd rib, measured from head to tip of costal cartilage, was 13·5 cm., and the measurement along its convex border, 21·5 cm. (8 in.).

The rudimentary 1st thoracic rib of the left side had very similar relations to those of the right. Its vertebral end articulated with the body and transverse process of the 8th vertebra, and its tip was connected by a fibrous cord with the pointed outer end of the 1st costal cartilage. Its tubercle articulated, however, with the transverse process of the 7th cervical vertebra as well as with that of the 8th vertebra. Owing, moreover, to the curvature of the vertebral column, the 1st left rib was not so highly curved as the 1st right rib, and the lower primary trunk of the brachial plexus passed outward below the level of the rib before crossing over the fibrous band, instead of bending over the rib, as on the right side. The subclavian artery also crossed the fibrous band and the 2nd rib beyond the tip of the 1st rib. The subclavian vein on both sides crossed over both the 2nd rib and the fibrous continuation of the 1st rib. The vertebral artery on the left side crossed in front of the neck of the rudimentary rib. The middle and upper primary trunks of the brachial plexus were situated immediately above the 1st rib, and lay in front of the middle scalene muscle, which was attached to the posterior part of the shaft of the 1st rib. The subclavian artery passed through the fibres of the anterior scalene muscle, some of which were attached to the tip of the 1st rib and adjacent part of the 2nd rib and others to the fibrous band, in front of the artery, between it and the vein.

Base of the skull

Intracranial aspect. The region around the foramen magnum and the adjoining parts of the petrosal elements of the temporal bones, appeared to have been pushed upwards from below into the cranial cavity, as if pressure on the head had been exerted in a downward direction against the resistance of the vertebral column pushing upwards from below, the base of the skull having yielded to the pressure and the counter-pressure.

The antero-posterior diameter of the foramen magnum was thus reduced from the normal 3·7 cm. to 2·3 cm., the greatest transverse diameter being 2·7 cm. The anterior condylar foramina were much reduced in size. The clinical history of the case, however, did not give any evidence of interference with the motor supply of the tongue. The odontoid process lay in a recess beneath the basioccipital and was overlapped on each side by the anterior margin of the foramen magnum. The left jugular foramen was almost obliterated; it transmitted the 9th, 10th and 11th cranial nerves, but neither the sigmoid sinus nor the inferior petrosal sinus passed through it. The blood from the sigmoid sinus on the left side being unable to leave by the jugular foramen, appears to have escaped through a much enlarged mastoid foramen, fig. 2. A similar large mastoid foramen was present on the right side, but the venous parts of the right jugular foramen were not obliterated, and both the inferior petrosal sinus and the main stream from the sigmoid sinus appear to have left the skull through this foramen. The groove for the sigmoid sinus on the left side was situated entirely on the temporal bone, the petro-occipital suture lying 0·5 cm. behind it. The central part of the petrosal element of each temporal was so curved upward as to form two prominences in the base of the skull.

Extracranial aspect. The region around the margin of the foramen magnum was hollowed in correspondence with the projection of the same region in the interior. There was a raised ridge round the lateral and posterior boundaries of the foramen magnum like that seen in cases of manifestation of the neural arch of an occipital vertebra. There were no posterior condylar foramina. The bone forming the floor of the cerebellar fossa on each side was extremely thin and translucent.

The cervical vertebrae

The atlas vertebra was smaller and more slender than the normal bone. Owing to the upward displacement of the central part of the bone into the hollow on the under-surface of the occipital bone, the transverse processes sloped obliquely downwards.

The axis, 3rd, 4th and the greater part of the 5th cervical vertebrae were fused into a single piece, figs. 1 and 2. This piece articulated with a block formed by the left half of the neural arch of the 5th cervical vertebra and the 6th, 7th and 8th vertebrae. An accessory joint, see fig. 1, was formed between these two blocks.

Case IX. Bilateral cervical ribs found in an aged female dissecting-room

subject. The atlas was fused with a partially separated occipital vertebra, and there was considerable asymmetry and obliquity of the upper cervical vertebrae and skull, the left transverse process of the atlas being half an inch lower than the right. A detailed description of the atlas and occipital bone of this case has been previously described by one of us, R. J. G., and Erichsen Powell in this *Journal* (1915). It serves as an illustration of variations in the vertebral column taking place in two directions, namely, shortening of the cervical region at the upper end by fusion of the atlas with an occipital vertebra, and at the lower end by the development of a pair of ribs on the 7th cervical vertebra. It is also an example of the co-existence in the same subject of manifestation of an occipital vertebra and fusion of the atlas with this vertebra and thus with the base of the skull.

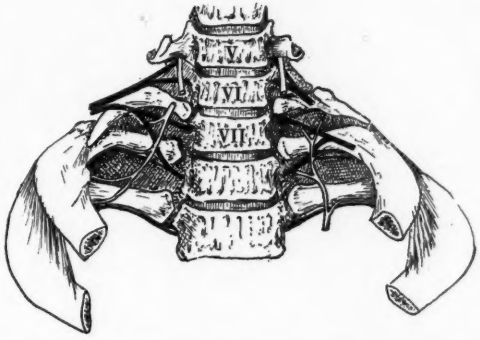

Fig. 11. Case IX. Drawing showing relation of nerves and vessels to cervical ribs.

The right cervical rib of this woman was 5 cm. long. It articulated by its head, with the body of the 7th cervical vertebra, and by its tubercle with the transverse process of the same vertebra. Its shaft was crossed obliquely on its upper surface by the lower primary trunk of the brachial plexus (fig. 11). This was formed by the union of the anterior primary divisions of the 8th cervical and 1st thoracic nerves. Above and behind this trunk was a trunk formed by the union of the 6th with the 7th cervical nerves. The subclavian artery crossed the rib in front of the lower primary trunk, and the subclavian vein passed over a fibrous cord which joined the tip of the cervical rib with the 1st thoracic rib. The costo-cervical artery on both sides of the body descended in front of the neck of the cervical rib. It then gave off the deep cervical branch which passed as usual in a backward direction between the transverse process of the 7th cervical vertebra and the neck of the 1st thoracic rib. Its intercostal branch on the right side descended in front of the 1st and 2nd thoracic ribs, and supplied the 1st and 2nd intercostal spaces. On the left side these spaces were chiefly supplied by an ascending branch from the aorta. This anastomosed in the 1st thoracic intercostal space with the left superior intercostal artery. The

vertebral artery on both sides entered the foramen transversarium of the corresponding side of the 5th cervical vertebra.

The left cervical rib was 3·5 cm. long, and deeply grooved on its upper surface by a nerve trunk formed by the union of the anterior primary divisions of the 6th and 7th cervical nerves. The lower primary trunk formed by the union of the 8th cervical and 1st thoracic nerves lay entirely below the cervical rib and crossed a fibrous cord which connected its tip with the 1st thoracic rib. The subclavian artery and the subclavian vein crossed the first thoracic rib in front of the cervical rib.

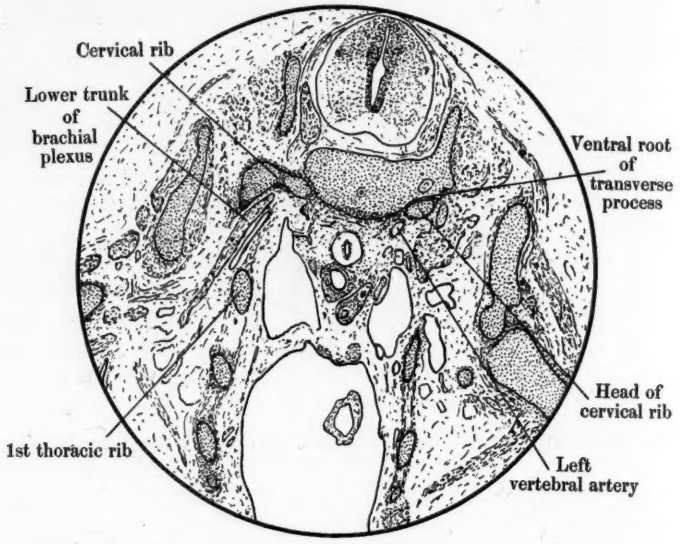

Fig. 12. Transverse section through a 19 mm. human embryo, showing the vertebral ends of a pair of 7th cervical ribs. On the left side, the ventral root of the transverse process of the 7th cervical vertebra is seen to be formed independently of the head and neck of the cervical rib.

Case X. Bilateral cervical ribs in a human embryo 19 mm. in length. This specimen was obtained by one of us, C. P. G. W., at a laparotomy, and is in excellent condition. The sections were made transversely. Differentiation of the gonads and adnexa was sufficiently advanced to recognise the sex as being female. The cervical rib on each side extended about one-third the distance from the vertebral column to the sternal bar of the corresponding side.

On the right side the ventral end of the cervical rib tapered to a point, which was connected to the cartilage of the 1st thoracic rib by a band of condensed mesoderm. It articulated by its head with the body of the 7th cervical vertebra and by its tubercle with the transverse process of this vertebra. A complete foramen transversarium was present in the transverse process of the 7th cervical vertebra on both sides, its anterior boundary being formed by a

cartilaginous bridge, continuous with the cartilage of the centrum medially and with the transverse process dorso-laterally, fig. 12; the foramen on each side transmitted a small vein. The anterior tubercle and the cartilaginous bridge forming the anterior wall of the foramen were separated from the head and neck of the cervical rib by perichondrial mesoderm, and the two structures were quite independent. The vertebral end of the left cervical rib had similar relations to that of the right, but the cartilage of its shaft was directly continuous at its ventral end with that of the 1st thoracic rib, fig. 13.

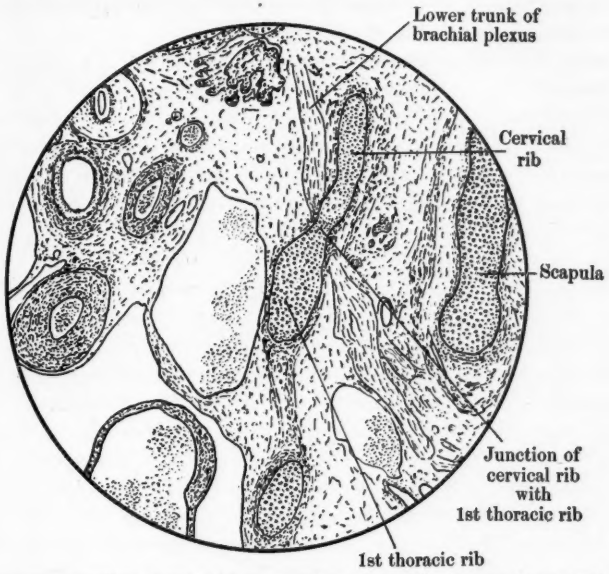

Fig. 13. Transverse section through the same embryo as fig. 12, showing the ventral end of the left cervical rib at its point of union with the 1st thoracic rib. It is probable that the continuity of the cartilage of the two ribs has been established secondarily.

The lower primary trunk of the brachial plexus on the right side crossed the cervical rib near its tip. It was formed by the junction of the anterior primary divisions of the 8th cervical and the 1st thoracic nerves. The subclavian artery and vein crossed the 1st thoracic rib, in front of the cervical rib. The first serration of the serratus anterior muscle as well as the scalenus medius muscle were attached to the cervical rib. The scalenus anterior was attached to the 1st thoracic rib in the usual situation between the subclavian arteries and veins. On the left side the general relations of the cervical rib were similar to those on the right, but the lower primary trunk of the brachial plexus crossed over the cartilaginous bar, which joined the sternal end of the cervical rib with the 1st thoracic rib.

There were eleven pairs of thoracic ribs, and six lumbar vertebrae. The vertebral arteries on each side entered the foramen transversarium on the corresponding side of the 6th cervical vertebra.

Variations of the transverse process of the 7th cervical and 1st dorsal vertebrae in the adult have been described by Duckworth and Dwight in the human subject, and by Bradley and Gorton in the horse. In the human embryo similar variations of the transverse processes of these vertebrae are also frequent. The 7th cervical vertebra, however, normally bears the cartilaginous rudiment of a cervical rib on each side. This rudiment, which represents merely the head, neck and tubercle of a cervical rib, frequently persists, as Struthers has shown, in the adult, but on account of its small size remains unrecognised. On the other hand, in the majority of cases, the rudiment either disappears by atrophy, or becomes fused with the transverse process.

The presence in the embryo of well-developed cervical ribs, with shafts extending forward towards the sternum, appears to be as unusual as it is in the adult. If this human embryo (case X), in which two well-developed cervical ribs were present, had survived, we consider that these ribs would have become ossified and remained in the adult in much the same condition as regards their relative size and relations, as they were in the embryo. There would have been a so-called "bicipital rib" on the left side, and a cervical rib of medium size ending in a fibrous band on the right side.

The anterior (costal) parts of the transverse processes of the upper cervical vertebrae are normally chondrified by an extension of the process of chondrification, from the true transverse process, joining the cartilage of the centrum, and an examination of the material which we have at our disposal shows that this is usually the case also in the 6th and 7th cervical vertebrae.

It is extremely improbable that the presence of well-developed cervical ribs in the adult is due, as has been suggested, to an arrest of the normal process of atrophy of embryonic cervical ribs, since the cervical ribs which are present in the embryo are a mere rudiment, and seldom extend beyond the tip of the transverse process. It is possible, however, that some cases of rudimentary 1st thoracic ribs may be due to atrophy of the central portion of a 1st thoracic rib, produced, as was suggested by Wood Jones, by pressure of the lower primary trunk of the brachial plexus, upon the developing rib. The close relationship of the roots of the brachial plexus to the 1st thoracic rib is well seen in fig. 14, which represents the condition found in the human embryo at the end of the 7th week of gestation. The part of the rib which is absent, however, is often much more extensive than could be accounted for, in this way, and on the other hand, cases occur in which the part of the rib which is crossed by the lower primary trunk is present and the anterior part only is missing.

Theories put forward in explanation of variations in the number and position of the ribs, and of meristic variations of the vertebral column

(1) *The ribs and pelvis are moved headward along the vertebral column, or in the reverse direction—tailward,* the total number of vertebrae remaining the same, but individual vertebrae are modified in adaptation to the changed position of the ribs or pelvis; the lumbo-sacral and brachial plexuses are also

assumed to be shifted forward (*pre-fixed type*), or backward (*post-fixed type*).

(2) *There is a tendency in Man and the higher Primates towards reduction in the number of ribs*, rudimentary 1st thoracic ribs or suppression of the last thoracic ribs being regarded as *progressive variations*, cervical ribs or lumbar ribs as *atavistic variations*.

(3) *Variations about a mean* which affect chiefly the transitional segments. When a vertebra of one region, such as the thoracic, assumes the special charac-

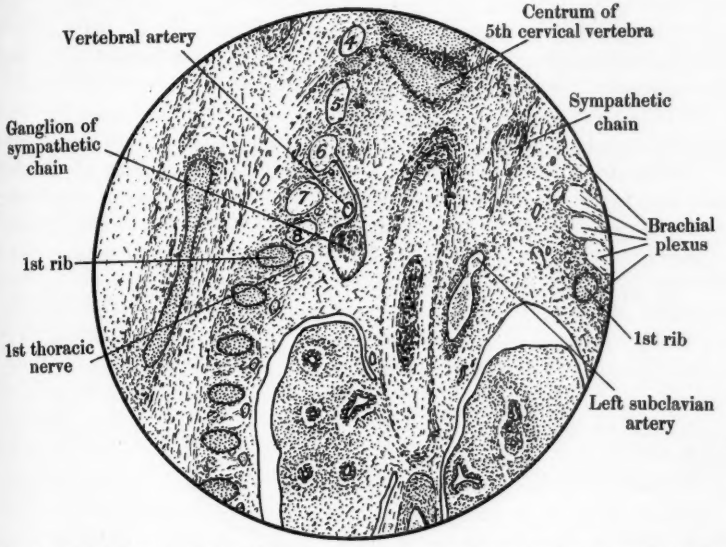

Fig. 14. Coronal section through a 20 mm. human embryo, showing the close relationship of the roots of the brachial plexus to each other, and the relation of these to the 1st thoracic rib.

ters of the region in front, e.g. the cervical, the variation was classed by Bateson as being a "*forward homoeosis*." When the vertebra of a particular region assumes the character of the vertebrae situated behind it, the condition is a "*backward homoeosis*"; thus, if the last pair of ribs is suppressed, the 12th thoracic vertebra will assume the characters of a lumbar vertebra (backward homoeosis); the development of a pair of cervical ribs is also an instance of backward homoeosis, the 7th cervical vertebra assuming the characters of a thoracic vertebra. The suppression of the 1st thoracic ribs is an example of forward homoeosis. Other examples of these changes will be given later, with reference to the bearing of this conception on the etiology of the variations.

(4) *The intercalation* of an additional vertebra and ribs between any two of a series, or *excalation*, of a vertebra with its accompanying costal elements.

In other words, addition to the total number, or suppression of one or more segments.

(5) *Irregularity in the cleavage* or segmentation of the body.

(6) *Fusion of segments*, as is common in the cervical region in cases of cervical ribs and rudimentary 1st thoracic ribs, and in cases of defective development of the vertebral column in teratological specimens.

In considering the causes of the changes met with in the adult skeleton, it must be remembered that some of these are secondary adaptive changes which have been brought about by attempts on the part of the organism to overcome the effects of the primary defect, e.g. compensatory curves of the vertebral column in congenital scoliosis produced by the suppression of half a vertebra, or modification of the atlo-axoidean articulation, to compensate for the loss of movement which results from fusion of the atlas with the occipital bone.

We have, however, been impressed in the study of these cases by the extreme frequency of defects of development, in association with cervical ribs and rudimentary 1st thoracic ribs, occurring in other regions of the body. These defects are not always directly dependent on the presence or absence of the ribs in question, or the accompanying variations in the vertebral column or spinal nerves, and it seems probable that there is a common cause which has produced an unstable condition of the body and which has affected the development of the skeletal and other systems. In other words a tendency to vary has been produced. A very considerable number of these variations come into the category of defective developments, and if, as seems probable, this is the true explanation of their occurrence, it is hardly conceivable that progressive evolution could take place by such irregular changes as are commonly met with in these cases. Many of the changes are obvious defects in development, and are sometimes incompatible with life, e.g. rachischisis or anencephalus.

Rudimentary 1st thoracic ribs may generally be distinguished from cervical ribs by paying attention to the following points, though it must be borne in mind that there are exceptions to the general rule, and that in some anomalous cases the right and left sides do not correspond, and that there may be a general irregularity and want of symmetry.

Facts that may be ascertained by X-ray examination:

Rudimentary 1st thoracic ribs

(1) Seven cervical vertebrae above the rudimentary 1st rib.

(2) The rib next below the rudimentary rib is long, and resembles a normal 2nd thoracic rib. Its length, including the costal cartilage being approximately 21 cm.

(3) The costal cartilage of a rudimentary 1st thoracic rib may be present as a separate part which articulates with the lateral angle of the manubrium in the ordinary situation of the 1st rib cartilage.

7th cervical ribs

(1) Six cervical vertebrae above the 1st rib.

(2) The rib next below the 1st rib is short and highly curved, and is more horizontally placed than is the 2nd rib in defective development of the 1st thoracic rib.

(3) A cervical rib rarely reaches the sternum, and if its tip does not end freely, it is joined to the 1st thoracic rib or its cartilage by a fibrous band, bone or cartilage.

Rudimentary 1st thoracic ribs

(4) The cartilage of the 2nd rib articulates either with the side of the manubrium, or joins the sternum at the joint between the manubrium and the body of the sternum.

(5) The cartilage of the 3rd rib usually joins the sternum below the level of the sternal angle, but the manubrium may be unusually long (7–8 cm.), owing to the inclusion in it of the 1st segment of the mesosternum, and it will then be joined on each side by three rib cartilages.

(6) Frequently eight pairs of rib cartilages articulate with the sternum.

(7) Twelve pairs of ribs are commonly present: occasionally thirteen.

(8) There may be twenty-five pre-sacral vertebrae, or the 1st sacral vertebra may be partially separated, and resemble a normal 5th lumbar vertebra.

7th cervical ribs

(4) The cartilage of the 2nd rib joins the lateral angle of the sternum in the usual situation of the cartilage of the 1st thoracic rib.

(5) The cartilage of the 3rd rib usually joins the sternum at the level of the sternal angle. If the 7th cervical rib is fully developed, three rib cartilages may articulate with a manubrium of normal length.

(6) Seven pairs of rib cartilages usually articulate with the sternum.

(7) Thirteen pairs of ribs are commonly present: in about one-third of the total number of cases twelve pairs are present. The last thoracic ribs are sometimes rudimentary, or may be absent.

(8) Usually twenty-four pre-sacral vertebrae.

Homoeotic variations

Bateson distinguished a separate group of variations, which he termed "homoeotic." In this category, one member of a meristic series assumes the form or characters proper to other members of the series, e.g. a cervical vertebra may bear ribs, and assume the characters of a dorsal vertebra. There is a substantive variation in the segment, but no alteration of its position in the series or in the total number of vertebrae. With reference to the vertebral column, the homoeosis may be in a forward direction towards the head or in a backward direction towards the tail end of the body. Thus Bateson distinguishes two types of homoeosis in the vertebral column:

(1) The alteration occurs in a direction from behind forwards—***Forward Homoeosis.***

(2) The alteration occurs in a direction from before backwards—***Backward Homoeosis.***

Examples of forward homoeosis:

Cervical to cranial	...	Fusion of atlas with occipital bone.
Dorsal to cervical	...	Rudimentary 1st thoracic rib.
Lumbar to dorsal	...	Lumbar ribs.
Sacral to lumbar	...	Liberation of 1st sacral vertebra.
Coccygeal to sacral	...	Fusion of 1st coccygeal vertebra with sacrum.

Examples of backward homoeosis:

Cranial to cervical	...	Manifestation of occipital vertebra.
Cervical to dorsal	...	Cervical ribs.
Dorsal to lumbar	...	Absence of 12th thoracic ribs.
Lumbar to sacral	...	Fusion of 5th lumbar vertebra with sacrum.
Sacral to coccygeal	...	Liberation of 5th sacral vertebra.

The terms employed in the examples cited are those which are most commonly used to designate the conditions described, and the authors wish it to be clearly understood that they do not want any inferences to be made from the suggestion indicated by the name of the cause of any particular variation, e.g. the term "sacralisation" of the 5th lumbar vertebra is more in accord with Bateson's description than the term usually employed to denote this condition, viz. fusion of the 5th lumbar vertebra with the sacrum.

In the case of suppression or rudimentary condition of the 1st thoracic ribs, the 1st thoracic vertebra assumes the characters of a 7th cervical, and the homoeosis is thus in a forward direction. In cervical ribs, the 7th cervical vertebra assumes the characters of the vertebra in the region next behind, namely, the 1st dorsal, and the homoeosis is thus backward.

The cases of cervical rib, rudimentary 1st thoracic rib and other variations in the number and position of the ribs which have been included in the following table, have for the most part been collected without selection from the cases published in the *Journal of Anatomy and Physiology*, and this *Journal* for a period of nearly 50 years, and though from the statistical standpoint their number may appear small, they are mostly cases in which the number of the ribs and their relation to the vertebrae have been described. They are therefore of much greater value than the records of a large number of clinical cases, in which the exact position of the abnormal rib or ribs relative to the vertebral column has not been stated. Four clinical cases in which scoliosis was present have been included, and also some anatomical cases, in which the whole of the vertebral column and ribs were not present. The authors, however, consider that these cases will help to substantiate rather than detract from, the value of the conclusions drawn from the more complete reports.

A short summary of associated conditions which have been present in the cases of congenital abnormalities of the ribs, is shown in the right-hand column of the following table. This clearly indicates the frequency with which defects, such as irregular formation of the vertebrae with congenital ankylosis and scoliosis, of the vertebral column, accompany the occurrence of cervical ribs, rudimentary 1st thoracic ribs, and other congenital variations in the number of the ribs.

The percentage frequency with which the defects mentioned below are associated with congenital variations in the number and position of the ribs, as recorded in the 70 cases which are reported, is 47·14; and the percentage frequency of cases in which it is definitely stated that spinal curvature or "scoliosis" was present, is 21·43. These figures are far too large to be explained by the assumption that a chance association of the two conditions has taken place, and a perusal of the total number of cases reported suggests that the abnormalities of the ribs and the associated defects may be related. These associated conditions belong to the category of defects of development, and include deformities, such as asymmetry of the face, cleft palate, hydrocephalus, spina bifida, talipes, fusion and irregularity of the ribs, asymmetry

Table I. *Table showing the frequency with which anomalies in the development of the ribs are associated with irregular*

Table I. *Table showing the frequency with which anomalies in the development of the ribs are associated with irregular segmentation of the vertebral column and other defects of development. The table also indicates the number of vertebrae in the regions denoted by the letters* C., *cervical;* T., *thoracic;* L., *lumbar;* S., *sacral. The position and number of the ribs on each side is also shown, and the number of ribs articulating with the sternum, when this has been recorded.* V., *vertebrae;* L.R., *left ribs;* R.R., *right ribs;* (*l.r.*), *rudimentary* 1*st thoracic rib;* + *unnumbered additional vertebrae;* M., *male;* F., *female*

Author		C.	T.	L.	S.	Total no. of ribs	No. of sternal ribs	Sex	Deformations
Addison	V.	7	12	—	—	—	—	F.	Costal cartilages of 1st thoracic ribs attached to side of manubrium, below a bony process at the lateral angle for the cervical rib
	L.R.	7th C.	12	—	—	13	—		
	R.R.	7th C.	12	—	—	13	—		
Babcock	V.	7	12	—	—	—	—	—	Scoliosis. Wasting and ischaemia. Asymmetry of face. Gangrene of fingers
	L.R.	—	12	—	—	12	—		
	R.R.	7th C.	12	—	—	13	—		
Barclay-Smith	V.	8	12	5	5	—	—	F.	Atlas fused with occipital bone. Axis and 3rd cervical vertebrae fused. 1st sacral vertebra partially lumbarised. Various minor malformations
	L.R.	8th C.	12	—	—	13	—		
	R.R.	—	12	—	—	12	—		
Bateson	V.	7	11	5	5	—	—	F.	5th and 6th cervical vertebrae partially ankylosed. 23 pre-sacral vertebrae
	L.R.	7th C.	11	—	—	12	—		
	R.R.	7th C.	11	—	—	12	—		
Bateson	V.	7	11	5	5	—	—	M.	23 pre-sacral vertebrae
	L.R.	7th C.	11	—	—	12	—		
	R.R.	7th C.	11	—	—	12	—		
Bellamy	V.	7	12	6	5	—	—	—	25 pre-sacral vertebrae. 1st thoracic ribs rudimentary. Quadratus femoris muscle absent
	L.R.	—	12(*l.r.*)	—	—	12	—		
	R.R.	—	12(*l.r.*)	—	—	12	—		
Black	V.	7	12	5	5	—	—	F.	
	L.R.	7th C.	12	—	—	13	—		
	R.R.	7th C.	12	—	—	13	—		
Brash	V.	6½	13	5	5	—	—	M.	Fusion and irregularity of cervical vertebrae. Ankylosis of thoracic vertebrae. Absence of half a vertebra in cervical region, with associated defect of spinal cord and absence of spinal nerves. Addition of whole segment in thorax
	L.R.	—	13	—	—	13	—		
	R.R.	—	13	—	—	13	—		

Table I (*continued*)

Author		C.	T.	L.	S.	Total no. of ribs	No. of sternal ribs	Sex	Deformations
Cleland	V.	6	12	6	—	—	—	F.	Cervical spina bifida. Cleft palate. Dorsal and cervical vertebrae much altered. Mesial gap between right and left halves of bodies of vertebrae, extending from 7th cervical vertebra up to axis. Fusion of laminae from 2nd to 5th cervical vertebrae
	L.R.	—	12	—	—	12	—		
	R.R.	—	12	—	—	12	—		
Dagnini	V.	7	12	—	—	—	—	M.	Head held at slight angle to prevent pain. Vasomotor disturbances due to pressure. Right arm and right cheek abnormally hot
	L.R.	7th C.	12	—	—	13	—		
	R.R.	7th C.	12	—	—	13	—		
De Vernejoul et Chauvin	V.	7	12	—	—	—	—	—	Scoliosis in cervico-dorsal region
	L.R.	7th C.	12	—	—	13	—		
	R.R.	—	12	—	—	12	—		
Dow (A)	V.	7	12	5	5	—	—	M.	Cartilages of 2nd thoracic ribs attached obliquely along the lateral border of the manubrium
	L.R.	—	12(*l.r.*)	—	—	12	—		
	R.R.	—	12(*l.r.*)	—	—	12	—		
Dow (B)	V.	7	12	—	—	—	—	—	Cartilages of 2nd thoracic ribs attached to lateral border of manubrium. Right vertebral artery entered transverse process of 5th cervical vertebra
	L.R.	—	12(*l.r.*)	—	—	12	—		
	R.R.	—	12(*l.r.*)	—	—	12	—		
Dukes and Owen	V.	7	12	5	—	—	—	—	2nd and 3rd cervical vertebrae fused. Costal element of transverse process of atlas ligamentous on right side
	L.R.	—	12(*l.r.*)	—	—	12	—		
	R.R.	—	12(*l.r.*)	—	—	12	—		
Dwight (A) Class III, Group C, V. fulcralis, 27	V.	7	13	6	5	—	—	—	Ribs 1–3 fused. Marked scoliosis. Laminae of cervical vertebrae very much distorted, several mingling together with their neighbours of the same side and not being opposite their fellows. 6th lumbar vertebra partially sacralised
	L.R.	—	13	—	—	13	—		
	R.R.	—	13	—	—	13	—		
Dwight (B) Class III, Group C, V. fulcralis, 27	V.	7	13	6	5	—	—	M.	Axis fused with 3rd cervical vertebra. Laminae so fused that it must be considered a congenital condition. 6th lumbar vertebra partially sacralised
	L.R.	—	13	—	—	13	—		
	R.R.	—	13	—	—	13	—		
Dwight (J) Class IV, Group C, H 3	V.	6	12	6	6	—	—	F.	Last lumbar vertebra sacralised on left side. Atlas and axis fused. 6th cervical vertebra resembles normal 7th. 7th cervical vertebra resembles normal 1st thoracic. Right 1st rib resembles normal 1st thoracic rib
	L.R.	—	12(*l.r.*)	—	—	12	—		
	R.R.	—	12(*l.r.*)	—	—	12	—		
Dwight	V.	7	12	5	6	—	—	—	4th and 5th cervical vertebrae fused. Irregularity and asymmetry
	L.R.	7th C.	12	—	—	13	—		
	R.R.	7th C.	12	—	—	13	—		

Table I (*continued*)

Author		C.	T.	L.	S.	Total no. of ribs	No. of sternal ribs	Sex	Deformations
Dwight	V.	7	12	—	—	—	—	—	Atlas and axis vertebrae fused. Irregularity of vertebrae
	L.R.	7th C.	12	—	—	13	—		
	R.R.	7th C.	12	—	—	13	—		
Edington	V.	7	11½	—	—	—	—	M.	Atresia ani. Absence of left kidney and ureter. Right alveolo-labial hare lip. Dwarfing of right thumb. Scoliosis. Fusion of vertebrae.
	L.R.	6 and 7	12	—	—	14	9		
	R.R.	7	11	—	—	12	8		Absence of right half of centrum of 5th thoracic vertebra. Fusion and irregularity of thoracic ribs. 6th and 7th left cervical ribs. 7th right cervical rib
Gaucher et Crouzon	V.	7	12	—	—	—	—	—	Congenital syphilis. Premature birth. Wassermann +. History of miscarriages in mother. Deafness. Interstitial keratitis. Peri-orbital pains
	L.R.	7th C.	12	—	—	13	—		
	R.R.	7th C.	12	—	—	13	—		
Gladstone and Wakeley	V.	7	13	5	5	—	—	M.	Fusion of cervical vertebrae 2–7 and 5–7. Scoliosis. Asymmetry and irregularity of skull. Supernumerary renal vessels. Low position of left kidney
	L.R.	—	13(*l.r.*)	—	—	13	7 (2–8)		
	R.R.	—	13(*l.r.*)	—	—	13	7 (2–8)		
Gladstone and Wakeley	V.	7	13	5	5	—	—	F.	Synostosis of atlas with occipital bone. Asymmetry and irregularity of vertebrae
	L.R.	7th C.	12	—	—	13	—		
	R.R.	7th C.	12	—	—	13	—		
Gladstone and Wakeley 19 mm. human embryo	V.	7	11	6	5	—	—	F.	Excess of pericardial fluid and irregular formation of thoracic wall
	L.R.	7th C.	11	—	—	12	—		
	R.R.	7th C.	11	—	—	12	—		
Goodhart (1)	V.	6½	11½	5½	—	—	—	M.	Atlas and occipital bone fused. Axis and 3rd cervical vertebrae fused and 7th cervical vertebra fused with 1st dorsal vertebra. 1st and 3rd left costal cartilages did not reach sternum. Body of 1st left vertebra absent. Spinal curvature, defective development of left arm and hand
	L.R.	(1)	12	—	—	13	7		
	R.R.	—	12	—	—	12	8		
Goodhart (2) foetal skeleton	V.	5½	12	—	—	—	—	M.	Spina bifida. Scoliosis. Defective development of occipital bone. Hydrocephalus. Talipes of both feet. 2nd and 3rd dorsal vertebrae fused. Irregularity in form
	L.R.	—	11	—	—	11	—		
	R.R.	—	11	—	—	11	—		
Goodhart (3)	V.	—	—	—	—	—	—	—	Fusion and irregularity of dorsal vertebrae, with fusion of laminae and spine. Scoliosis
	L.R.	—	—	—	—	—	—		
	R.R.	—	—	—	—	—	—		

Table I (*continued*)

Author		C.	T.	L.	S.	Total no. of ribs	No. of sternal ribs	Sex	Deformations
Harris	V.	7	11½	5	5	—	—	M.	Costal element of right transverse process of atlas ligamentous. 2nd and 3rd cervical vertebrae fused. Vertebral artery passes through 7th transverse process. Tracheo-oesophageal fistula. Stenosis of oesophagus. Imperforate anus. Vascular and cardiac anomalies. Absence of left kidney
	L.R.	—	10	1st L.	—	11	7		
	R.R.	—	12	—	—	12	7		
Helm	V.	—	—	—	—	—	—	—	Asymmetry of sternum. Right subclavian artery anterior to anterior scalene muscle. Accessory phrenic nerve
	L.R.	—	12	—	—	12	7		
	R.R.	—	12(*l.r.*)	—	—	12	8		
Hertslet and Keith (A)	V.	7	11	6	5	—	—	F.	Vertebral arteries enter 5th cervical vertebra
	L.R.	7th C.	11	—	—	12	—		
	R.R.	7th C.	11	—	—	12	—		
Hertslet and Keith (B)	V.	7	12	—	—	—	—	M.	Sternoscapular muscle. Stylohyoid ligament ossified. Levator anguli scapulae inserted into 2nd rib as well as into scapula
	L.R.	—	12(*l.r.*)	—	—	12	—		
	R.R.	—	12(*l.r.*)	—	—	12	—		
Jones	V.	7	12	(5)	(5)	—	—	F.	Costal cartilages of 1st and 2nd rib joined at their sternal extremities
	L.R.	—	12(*l.r.*)	—	—	12	8		
	R.R.	—	12(*l.r.*)	—	—	12	8		
Lane	V.	8	12	5	—	—	—	—	25 pre-sacral vertebrae. Lane considered that an extra vertebra was intercalated in the cervical region. The 1st rib had the usual appearance of a cervical rib
	L.R.	8th C.	12	—	—	13	—		
	R.R.	8th C.	12	—	—	13	—		
Leboucq	V.	8	12	5	5	—	—	—	2nd and 3rd cervical vertebrae fused. Leboucq considered the 3rd cervical to be the intercalated vertebrae
	L.R.	8th C.	12	—	—	13	—		
	R.R.	8th C.	12	—	—	13	—		
Lucas (I)	V.	7	12	—	—	—	—	F.	
	L.R.	7th C.	12	—	—	13	—		
	R.R.	7th C.	12	—	—	13	—		
Lucas (II)	V.	7	11	5	6	—	—	M.	Prefixed lumbar plexus
	L.R.	7th C.	11	—	—	12	—		
	R.R.	7th C.	11	—	—	12	—		

R.R. 7th C. 11 — — 12 —

Table I (*continued*)

Author		C.	T.	L.	S.	Total no. of ribs	No. of sternal ribs	Sex	Deformations
Macphail	V.	7	12	—	—	—	—	M.	Sternal end of left clavicle prolonged downward in a hook-shaped manner. Costal cartilages of 2nd ribs directed obliquely downward by the side of the manubrium. Muscular abnormalities
	L.R.	—	12(*l.r.*)	—	—	12	—		
	R.R.	—	12(*l.r.*)	—	—	12	—		
Morris	V.	7	—	—	—	—	—	—	Syringomyelia
	L.R.	7th C.	—	—	—	—	—		
	R.R.	7th C.	—	—	—	—	—		
Paterson and Lovegrove (I)	V.	7	12	6	4	—	—	—	Imperfect formation with irregularity in union of the neural arches in the cervical region. 6th and 7th left ribs fused near their vertebral ends
	L.R.	7th C.	12	—	—	13	—		
	R.R.	7th C.	12	1st L.	—	14	—		
Paterson and Lovegrove (II)	V.	7	13	6	5	—	—	—	Irregularity of neural arches in cervical region. Left half of 3rd and right half of 4th neural arches fused. Fusion of 6th and 7th left ribs
	L.R.	7th C.	12	—	—	13	—		
	R.R.	7th C.	13	—	—	14	—		
Phillips (I)	V.	7	12	5	5	—	—	M.	Spina bifida involving atlas and axis. 5th lumbar vertebra in two parts. Irregular union of costal cartilages with sternum. Manubrium 3 in. long
	L.R.	7th C.	12	—	—	13	7		
	R.R.	7th C.	12	—	—	13	8		
Phillips (II)	V.	7	12	5	5	—	—	F.	Irregularity of union of costal cartilages with sternum. 5th and 6th cervical vertebrae fused. Foramina in gladiolus and ensiform appendix
	L.R.	7th C.	12	—	—	13	7		
	R.R.	7th C.	12	—	—	13	7		
Railliet	V.	7	—	—	—	—	—	F.	Left side of face smaller than right. Enophthalmos. Left hemicrania. Teeth lost on left side. Mother nervous. Father alcoholic. Brother in an asylum. Asymmetry of face in an aunt. Right side of face atrophied in grandmother
	L.R.	7th C.	—	—	—	—	—		
	R.R.	7th C.	—	—	—	—	—		
Roederer	V.	7	—	—	—	—	—	—	Subluxation of left sternoclavicular joint. Scoliosis
	L.R.	7th C.	—	—	—	—	—		
	R.R.	7th C.	—	—	—	—	—		
Rosenberg	V.	7	13	6	—	—	—	—	
	L.R.	7th C.	13	1	—	15	—		
	R.R.	7th C.	13	1	—	15	—		

Table I (*continued*)

Author		C.	T.	L.	S.	Total no. of ribs	No. of sternal ribs	Sex	Deformations
Royal College of Surgeons of England 500. 3	V.	6½	12	5	—	—	—	—	Atlas ankylosed to occipital bone. Axis and 3rd cervical vertebrae fused. Left half of 7th cervical vertebra absent. In consequence 6th cervical vertebra has descended into contact with 1st dorsal vertebra and an angular curvature is present with concavity to left. The left transverse process of the 1st dorsal vertebra has assumed characteristics of the transverse process of a 7th cervical vertebra. 1st thoracic rib absent on left. Costal cartilages of 2nd and 3rd ribs inserted together into lateral angle of manubrium sterni in usual situation of 1st costal cartilage. The costal cartilage of the 4th rib joins sternum at junction of manubrium with body. Manubrium joined on right to 1st, 2nd and 3rd costal cartilages. 4th upper dorsal vertebra ankylosed. Lumbar vertebrae fused and irregular
	L.R.	—	11	1	—	12	2–8		
	R.R.	—	12	—	—	12	1–7		
Still	V.	7	12	5	5	—	—	F.	Costal cartilage of 4th and 5th ribs of left side join to form single broad cartilage attached to sternum. Arrested development of infundibular part of right ventricle of heart. Patent interventricular foramen and foramen ovale. Little fingers of both hands stunted. Mongoloid type. Blue baby
	L.R.	—	12	—	—	12	—		
	R.R.	—	11	—	—	11	—		
Struthers (I)	V.	7	4+	—	—	—	—	M.	Vertebral foramen on each side of 6th cervical vertebra completed by bar of bone which is independent of the neck of the rib. Vertebral foramen of transverse process of 7th cervical vertebra completed on left side by bar of bone, on right by ligament
	L.R.	6, 7	4+	—	—	? 14	—		
	R.R.	6, 7	4+	—	—	? 14	—		
Struthers (II)	V.	6, 7	2+	—	—	—	—	F.	Cervical ribs form entire anterior boundary of vertebral foramen
	L.R.	7th	2+	—	—	? 13	—		
	R.R.	7th	2+	—	—	? 13	—		
Struthers (III)	V.	7	12	5	5	—	—	—	The neck of each cervical rib bounds the transversarium foramen
	L.R.	7th	12	—	—	13	—		
	R.R.	7th	12	—	—	13	—		
Struthers (IV)	V.	7	1+	—	—	—	—	—	7th cervical rib of left side ankylosed to transverse process. Right cervical rib movable
	L.R.	7th	1+	—	—	? 13	—		
	R.R.	7th	1+	—	—	? 13	—		
Struthers (V)	V.	7	12	5	5	—	—	F.	7th cervical rib of left side free, ankylosed rib on right side. 12th thoracic ribs small. Atlas has posterior bridge on both sides
	L.R.	7th	12	—	—	13	—		
	R.R.	7th	12	—	—	13	—		

Table I (*continued*)

Table I (*continued*)

Author		C.	T.	L.	S.	Total no. of ribs	No. of sternal ribs	Sex	Deformations
Struthers (VI)	V.	7	—	—	—	—	—	—	Laminae of atlas ununited. Cervical rib on left side free, on right side ankylosed externally
	L.R.	7th	—	—	—	—	—		
	R.R.	7th	—	—	—	—	—		
Struthers (VII *a*)	V.	7	—	—	—	—	—	F.	7th cervical vertebra has, on right side, notch for head of thoracic rib
	L.R.	7th	—	—	—	—	—		
	R.R.	7th	—	—	—	—	—		
Struthers (VII *b*)	V.	7	—	—	—	—	—	F.	
	L.R.	7th	—	—	—	—	—		
	R.R.	7th	—	—	—	—	—		
Struthers (VIII)	V.	7	12	5	5	—	—	M.	Existence of cervical ribs inferred from the presence of facets for them on the body and transverse processes of the 7th cervical vertebra. Lateral foramen appears to be wanting
	L.R.	7th	12	—	—	13	—		
	R.R.	7th	12	—	—	13	—		
Struthers (IX)	V.	—	—	—	—	—	—	F.	Cervical rib resting by its anterior end on a cornual process of the 1st thoracic rib. Recognised during life and removed post-mortem
	L.R.	7th	1+	—	—	—	—		
	R.R.	?	—	—	—	—	—		
Struthers (X)	V.	7	12	5	5	—	—	F.	Right cervical rib joined to cornual process on 1st thoracic rib. Left cervical rib reaches sternum. Left vertebral artery entered foramen in 5th cervical vertebra
	L.R.	7th	12	—	—	13	? 8		
	R.R.	7th	12	—	—	13	? 7		
Struthers (XI)	V.	—	—	—	—	—	—	F.	No symptoms. Visible pulsation of left subclavian artery
	L.R.	7th	—	—	—	—	—		
	R.R.	—	—	—	—	—	—		
Struthers (XII)	V.	—	—	—	—	—	—	M.	Visible pulsations of right subclavian artery
	L.R.	—	—	—	—	—	—		
	R.R.	7th	—	—	—	—	—		
Struthers (XIII)	V.	7	12	5	5	—	—	M.	1st and 2nd thoracic ribs on each side articulate with upper part of manubrium by a common cartilage. Fibrous band from the 1st rib on each side joins the tip of a cornual process of 1st rib cartilage. Manubrium long. 3rd rib cartilages join sternum at junction of manubrium and gladiolus
	L.R.	—	12(*l.r.*)	—	—	12	8		
	R.R.	—	12(*l.r.*)	—	—	12	8		

Table I (*continued*)

Author		C.	T.	L.	S.	Total no. of ribs	No. of sternal ribs	Sex	Deformations
Terry	V.	(7)	(12)	(5)	(5)	—	—	F.	Scoliosis. Metopic suture. Divided parietals. Wormian bones. Rudimentary clavicles. Manubrium divided into right and left halves by vertical suture. Gladiolus consists of four separate units. Contracted pelvis. Separation of lower from upper part of sacrum
	L.R.	—	12	—	—	12	8		
	R.R.	—	12	—	—	12	8		
Todd (A)	V.	7	11	6	5	—	—	M.	Atlas shows an ossified bridge over vertebral artery. There is a double foramen transversarium in the 6th cervical vertebra
	L.R.	7th C.	11	—	—	12	—		
	R.R.	7th C.	11	—	—	12	—		
Todd (B)	V.	7	12	5	—	—	—	M.	6th cervical vertebra asymmetrical. 1st left thoracic rib has a tubercle for articulation with the cervical rib
	L.R.	7th C.	12	—	—	13	—		
	R.R.	7th C.	12	—	—	13	—		
Todd (C)	V.	7	5	—	—	—	—	M.	Scoliosis. "Pathological changes have taken place in bodies and articular processes of cervical region producing scoliosis"
	L.R.	—	5 (*l.r.*)	—	—	—	—		
	R.R.	—	5 (*l.r.*)	—	—	—	—		
Todd (D)	V.	7	12	5	5	—	—	F.	
	L.R.	—	12	—	—	12	7		
	R.R.	7th C.	12	—	—	13	7		
Turner (A)	V.	7	12	—	—	—	—	M.	
	L.R.	7th C.	12	—	—	13	—		
	R.R.	7th C.	12	—	—	13	—		
Turner (B)	V.	7	12	—	—	—	—	F.	The spine of this old woman was greatly curved—the ribs distorted and the pelvis contracted
	L.R.	7th C.	12	—	—	13	—		
	R.R.	7th C.	12	—	—	13	—		
Turner (C)	V.	7	12	—	—	—	—	M.	
	L.R.	—	12	—	—	12	—		
	R.R.	7th	12	—	—	13	—		
Turner (D)	V.	7	12	5	—	—	—	M.	1st thoracic rib of left side so fused with 2nd thoracic rib, that this appeared bicipital. Sternal end was present, as cartilage attached to lateral angle of the sternum in normal situation of costal cartilage of 1st thoracic rib. This was connected with the 2nd rib and tip of the 1st rib by a fibrous cord

of the sternum and various abnormalities of the soft parts, as well as the above-mentioned defects of the vertebral column. The more important of these defects appear to arise as a primary disturbance of segmentation which has taken place at an early stage of development, and involved in some cases the neural tube, and the spinal nerves arising from it (Brash). Others are secondary results of the primary disturbance in segmentation. They may be purely adaptive, and take place during the intra-uterine growth of the embryo, or in some cases, in infancy or adult life.

An example of the former is the extension upwards, in certain cases of rudimentary 1st thoracic rib, of the attachment of the cartilage of the 2nd thoracic rib on the side of the sternum, so as to stabilise the manubrium, and compensate for the loss of support which is normally given to its lateral angle by a fully developed 1st thoracic rib. The same result may be obtained by the bending upward of the 2nd thoracic rib, so that the cephalic border of its costal cartilage will become attached to the lateral edge of the manubrium, and the size of the thoracic inlet at the same time becoming diminished, will thus approximate to the normal proportion (case VIII, of authors).

Some of the secondary changes are obviously not adaptive, but the result of an interference of the nerve or vascular supply of a developing organ, e.g. in the case of suppression of one half of a vertebra with absence of the corresponding rib, and intercostal structures, including the somatic and splanchnic nerves. In such a case there may be loss of tone in the wall of the corresponding segment of the intestine, followed by an interruption of the peristaltic wave, and dilatation of the part beyond.

Table II. *Cervical ribs* (32 *cases*)

Author	M.	F.	Author	M.	F.
Addison	—	1	Struthers	1	—
Barclay-Smith	—	1	,,	—	1
Bateson	—	1	,,	—	1
,,	1	—	,,	1	—
Black	—	1	,,	—	1
Brash	1	—	,,	—	1
Dagnini	1	—	,,	—	1
Edington	1	—	,,	—	1
Gladstone and Wakeley	—	2	,,	1	—
Hertslet and Keith	—	1	Todd	1	—
Lucas	—	1	,,	1	—
,,	1	—	,,	—	1
Phillips	1	—	Turner	1	—
,,	—	1	,,	—	1
Railliet	—	1	,,	1	—
Struthers	—	1			

Total: M. 13, F. 19.

Table III. *Rudimentary 1st thoracic ribs* (9 *cases*)

Author	M.	F	Author	M.	F.
Dow	1	—	Macphail	1	—
Dwight	—	1	Struthers	1	—
Gladstone and Wakeley	1	—	Todd	1	—
Hertslet and Keith	1	—	Turner	1	—
Jones	—	1			

Total: M. 7, F. 2.

Table IV. *Cervical ribs and rudimentary 1st thoracic ribs* (41)

M.	F.
20	21

Table V. *Irregular formation and ankylosis of vertebrae associated with cervical ribs, rudimentary 1st thoracic ribs, or other variations in the number of ribs* (70)

Author	No. of cases	Author	No. of cases
Babcock	1	Lane	1
Barclay-Smith	1	Leboucq	2
Bateson	1	Paterson and Lovegrove	2
Brash	1	Phillips	2
De Vernejoul et Chauvin	1	R.C.S. Eng. 500. 3	1
Dukes and Owen	1	Struthers	1
Dwight	5	Terry	1
Edington	1	Todd	2
Gladstone and Wakeley	2	Turner	1
Goodhart	2	Wakeley	3
Harris	1		

Total no. of cases, 33. Percentage no. 47·14.

Table VI. *Congenital scoliosis of vertebral column, associated with congenital variations in the number of ribs* (70)

Author	No. of cases	Author	No. of cases
Babcock	1	Goodhart	2
Dagnini	1	Roederer	1
De Vernejoul et Chauvin	1	Todd	1
Dwight	1	Turner	1
Edington	1	Wakeley	3
Gladstone and Wakeley	2		

Total no. of cases, 15. Percentage no. 21·43.

Table VII. *Cases in which it was recorded that eight or nine ribs articulated with the sternum*

Author	Cervical rib	Rudimentary 1st thoracic rib
Edington	(2)	—
Helm	—	(1)
Jones	—	(2)
Phillips	(1)	—
Struthers	—	(2)
Total (5)	2 cases	3 cases

Table VIII. *Cases in which it was recorded that seven ribs, from 2nd to 8th, articulated with the sternum*

Author	Cervical rib	Rudimentary 1st thoracic rib
Gladstone and Wakeley	—	(2)
Royal College of Surgeons	—	(1)
Total (2)	—	2

The numeral (1) indicates that the condition is unilateral, (2) that the condition is bilateral.

According to these tables it appears that 7th cervical ribs are more commonly present than rudimentary 1st thoracic ribs, that cervical ribs are more commonly present in the female than in the male, and a rudimentary condition of the 1st thoracic rib is relatively more common in the male sex. This accords with the general opinion based on clinical observations but the number

Table IX. *Cases of cervical ribs in which the total number of ribs and their relation to the vertebral column has been recorded*

	Total no. of left ribs					Total no. of right ribs					
Author	11	12	13	14	15	11	12	13	14	15	
Addison	.	.	+1	.	.	.	.	+1	.	.	Bilateral
Babcock	.	1	.	.	.	.	.	+1	.	.	Unilateral
Barclay Smith	.	1	.	.	.	.	.	+1	.	.	,,
Bateson	.	1	.	.	.	.	1	.	.	.	Bilateral
,,	.	1	.	.	.	.	1	.	.	.	,,
Black	.	.	+1	.	.	.	.	+1	.	.	,,
Dagnini	.	.	+1	.	.	.	.	+1	.	.	,,
De Vernejoul et Chauvin	.	.	+1	.	.	.	1	.	.	.	Unilateral
Dwight	.	1	.	.	.	.	1	.	.	.	Bilateral
,,	.	1	.	.	.	.	1	.	.	.	,,
Edington	.	.	.	+1	.	1	.	.	.	.	,,
Gaucher et Crouzon	.	.	+1	.	.	.	1	.	.	.	Unilateral
Gladstone and Wakeley	.	.	+1	.	.	.	.	+1	.	.	Bilateral
,, ,,	.	1	.	.	.	.	1	.	.	.	,,
Goodhart	.	.	+1	.	.	.	1	.	.	.	Unilateral
Hertslet and Keith	.	1	.	.	.	.	1	.	.	.	Bilateral
Lane	.	.	+1	.	.	.	.	+1	.	.	,,
Leboucq	.	.	+1	.	.	.	.	+1	.	.	,,
,,	.	.	+1	.	.	.	.	+1	.	.	,,
Lucas	.	.	+1	.	.	.	.	+1	.	.	,,
,,	.	1	.	.	.	.	1	.	.	.	,,
Paterson and Lovegrove	.	.	+1	.	.	.	.	+1	.	.	,,
Phillips	.	.	+1	.	.	.	.	+1	.	.	,,
,,	.	.	+1	.	.	.	.	+1	.	.	,,
Rosenberg	.	.	.	.	+1+ +	.	.	.	.	+1+ +	,,
Struthers (III)	.	.	+1	.	.	.	.	+1	.	.	,,
,, (V)	.	.	+1	.	.	.	.	+1	.	.	,,
,, (VIII)	.	.	+1	.	.	.	.	+1	.	.	,,
,, (X)	.	.	+1	.	.	.	.	+1	.	.	,,
Todd	.	1	.	.	.	.	1	.	.	.	,,
,,	.	.	+1	.	.	.	.	+1	.	.	,,
,,	.	1	.	.	.	.	.	+1	.	.	Unilateral
Turner	.	.	+1	.	.	.	.	+1	.	.	Bilateral
,,	.	.	+1	.	.	.	.	+1	.	.	,,
,,	.	1	.	.	.	.	.	+1	.	.	Unilateral
	.	12	21	1	1	1	11	22	—	1	Bilateral 28
											Unilateral 7

The + mark placed on the left side of the figure in a column indicates that the additional rib or ribs were considered to be cervical. The + mark on the right side of the figure indicates the presence of lumbar ribs. The table shows that there is an increase in the total number of ribs in cases of cervical ribs in approximately $\frac{2}{3}$ of the total number of cases.

of cases recorded is obviously too small to make a final statement with regard to sex frequency. It will be observed, however, Table IV, that when the figures relating to sex frequency in the two types of cases (cervical ribs, and rudimentary 1st thoracic ribs) are combined, the ratios are almost equal.

Records of observations on the exact relations of the ventral ends of the ribs to the sternum in cases of rudimentary 1st thoracic ribs and 7th cervical ribs

are unfortunately too few for any statistical statement to be of much value. We consider however that more attention should be paid to this relation than has been the case hitherto. Clinically it is of importance to distinguish the two conditions one from the other. From the morphological standpoint the very occasional presence of a triangular plate of cartilage attached to the lateral angle of the manubrium sterni in cases of incomplete 7th cervical rib offers a morphological problem which is of considerable interest in connection with the developmental relation of the ventral ends of the ribs to the sternum. This question we propose to consider fully in a subsequent contribution dealing with the origin and development of the sternum.

Table X. *Cases of rudimentary 1st thoracic ribs in which the total number of ribs and their relation to the vertebral column has been recorded*

	Total no. of left ribs					Total no. of right ribs				
Author	11	12	13	14	15	11	12	13	14	15	
Bellamy	.	−1	.	.	.	.	−1	.	.	.	Bilateral
Dow	.	−1	.	.	.	.	−1	.	.	.	,,
,,	.	−1	.	.	.	.	−1	.	.	.	,,
Dukes and Owen	.	−1	.	.	.	.	−1	.	.	.	,,
Dwight	.	−1	.	.	.	.	−1	.	.	.	,,
Gladstone and Wakeley	.	.	−1	.	.	.	.	−1	.	.	,,
Helm	.	+1	.	.	.	.	−1	.	.	.	Unilateral
Hertslet and Keith	.	−1	.	.	.	.	−1	.	.	.	Bilateral
Jones	.	−1	.	.	.	.	−1	.	.	.	,,
Macphail	.	−1	.	.	.	.	−1	.	.	.	,,
Struthers	.	−1	.	.	.	.	−1	.	.	.	,,
Turner	.	−1	.	.	.	.	+1	.	.	.	Unilateral
Total	.	−10	−1	.	.	.	−10	−1	.	.	Bilateral 10 Unilateral 2

The − mark placed to the left of a figure indicates a rudimentary condition of the 1st thoracic rib on the side indicated. If a + sign is present the 1st thoracic rib is complete on that side. The table shows that lumbar ribs are only occasionally present in cases of rudimentary 1st thoracic ribs.

Table XI. *Cases in which thirteen pairs of ribs have been present, the additional ribs having been recorded as 8th cervical: in which also an additional presacral vertebra was present, and was regarded as an intercalated cervical vertebral*

	Ribs		
Author			
Lane	8th cervical	12 T.	Bilateral
Lebouceq	,,	12 T.	,,
,,	,,	12 T.	,,

SUMMARY OF CLINICAL OBSERVATIONS AND RESULTS OF TREATMENT

The symptoms caused by cervical ribs are those due to pressure upon the subclavian artery and brachial nerve trunks. As a rule the shorter ribs are more prone to cause pressure on the brachial plexus, and the longer ones to cause compression of the subclavian artery. The rib can be exposed by an incision along the posterior border of the sterno-mastoid muscle and if a bigger exposure is necessary, the incision may be prolonged outwards along the upper

border of the inner third of the clavicle. The scalenus anticus muscle is exposed and divided at its insertion. This procedure itself may be all that is required; however, if there is still some pressure on the artery or nerves, the anterior part of the rib is excised subperiosteally; by so doing no important structures are injured.

The results of operations for relief of symptoms in cases of cervical ribs are not uniformly good, especially where the brachial plexus has been pressed upon. This is due to the fact that the pressure on the nerves has been of long standing and only partial recovery can be anticipated.

In some cases an enlarged and elevated 1st thoracic rib may of itself produce symptoms similar to those of a cervical rib, especially if it is situated

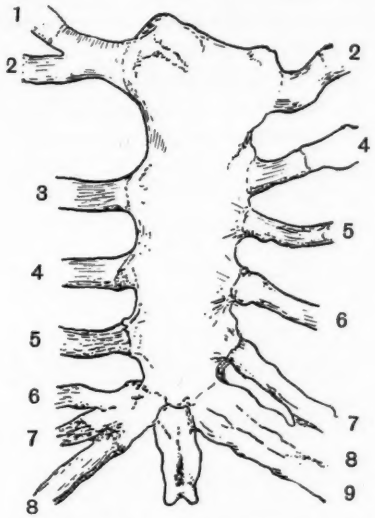

Fig. 15. Sternum and costal cartilages of a skeleton in which there was great irregularity, associated with defective development and fusion of the vertebrae and ribs. The 1st and 3rd ribs of the left side failed to reach the sternum. The specimen illustrates the apparently fortuitous manner in which the ribs may join the sternum under these conditions.

nearer the brachial plexus than usual. In these cases, removal of the middle third of the rib subperiosteally, will generally free the patient from all symptoms.

The study of the relation of abnormal ribs to the sternum (see fig. 15) is one which involves the study of the normal relations of the developing ribs and sternum to each other, not only in Man, but in all classes of vertebrate animals. At the present time, the opinions of morphologists and various workers who have been studying the ontogeny of the sternum differ in a most fundamental manner. We have, therefore, devoted a considerable amount of time and attention to the study of the chief points at issue from the palaeontological,

comparative and ontogenetic aspects, in the hope of coming to a final conclusion as to the extent to which the shoulder girdle, ribs, and somatic mesoderm are concerned in the development of the sternum in Man, and representative types of various vertebrate animals.

A part of this work has already been communicated to the Anatomical Society at the last meeting, held at King's College, London, in June 1931. At this meeting, slides were shown illustrating the history of its development as indicated by the ventral median cartilages of certain Fishes; various types of sternal apparatus in Amphibia, and Reptiles, including the bilateral elliptical bony plates found in certain extinct Reptiles; and also representative forms of sternum in Birds and Mammals. Models of the developing sternum of a mouse and of a rabbit embryo illustrating the relation of the ribs to the sternum in the *prochondral* and early *chondral* stages were also shown, and the development of the sternum in these rodents described.

A general description of the ontogeny of the sternum and the varying relations of the ribs to the sternum in Man and different types of vertebrate animals is obviously too extensive a subject to be dealt with in this paper. The authors have, therefore, decided to postpone the discussion of this matter and its relation to abnormalities of the ribs for a communication which will be published as a sequel to the present paper.

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SOME VARIATIONS IN THE LOWER END OF THE FEMUR WHICH ARE ESPECIALLY PREVALENT IN THE BONES OF PRIMITIVE PEOPLE

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From time to time attention has been drawn by several workers to various features in the form of the bones of the lower limb in primitive people which are not usually found in those of civilised races. Instances of these are squatting facets at the lower end of the tibia and on the neck of the talus, greater convexity of the articular surface of the lateral condyle of the tibia, flattening of the tibia and of the femur, retroversion of the head of the tibia and others, all these conditions being characteristic of the bones of relatively primitive races. These structural variations are accounted for by different habits of life followed by two classes of people, and especially by the difference in the usual resting posture; primitive individuals generally squat, whereas civilised individuals generally sit. But, with the single exception that in the femora of squatting people the articular surface of the medial condyle of the femur extends more on to the upper surface than in the case of non-squatters (1), none of the variations hitherto described refer to the lower end of the femur.

The present work originated in a routine examination of some freshly dissected knee-joints in the Anatomy School, Trinity College, Dublin. From this examination I was led to think that in certain definite particulars the lower end of the femur in primitive people might be expected to differ from that of a modern civilised individual. This induced me to carry out a systematic inspection of a number of early Irish femora which were found associated with tibiae bearing well-marked squatting facets, and to make a comparison of them with modern Irish specimens. As this inspection and comparison appeared to confirm my suspicions I studied all the available femora in Trinity College, including both those from modern Irish and from primitive races. These collections, however, were too small to serve as a basis from which general conclusions could be drawn, consequently, through the courtesy of Sir Arthur Keith, I subsequently examined the specimens preserved in the Museum of the Royal College of Surgeons, London.

Before dealing with the actual results obtained some preliminary considerations may perhaps be discussed. The knee-joint has the greatest range of movement of any of the joints of the lower limb. It therefore seems reasonable to expect that any considerable change in habit of life would be reflected by changes in form and structure especially in the neighbourhood of this joint.

Obviously the squatting attitude must put a very special strain on the structures in this region, and since, as stated above, some variations of the upper end of the tibia found in primitive people have been correlated with the use of the squatting posture, we would expect to find the lower end of the femur affected to a greater extent than the single very slight modification of the medial condyle mentioned above. Apart, however, from the use of the squatting position modern civilised races lead a much less active life than either primitive tribes or their own hunting ancestors, and we might expect this change would bring about some variation in form. Of course it must be borne in mind that many individuals even in the most civilised races are very active, and many workpeople in such races squat, or which is almost the same thing, sit on their heels while at work, so some femora from civilised people will probably conform fairly closely to those from more primitive races. Still, on the whole, the change both in general activity and in the usual resting posture is quite definite and this fact suggests that corresponding changes in form should be observable.

THE INTERCONDYLAR FOSSA

When a dissected knee-joint, in which all the surrounding structures have been removed leaving only the two cruciate and the tibial and fibular collateral ligaments in place, is put in the fully flexed position and examined from behind, it can be seen that the posterior cruciate ligament is tightly stretched and, as the extreme degree of flexion is reached, the ligament is pressed against the posterior aspect of the femur at the medial side of the intercondylar fossa, or rather at the junction of the floor of this fossa with the popliteal surface of the bone. This junction is marked by a distinct ridge: the intercondylar line, which in specimens from modern civilised races is usually very prominent and situated a short distance below the level of the upper surfaces of the condyles. It is slightly convex upwards and is equally well developed throughout its whole length from the medial to the lateral condyle. There is generally a sharp "step down" from the intercondylar line to the popliteal surface of the bone. In the dissected joint it can be seen that the attachment of the anterior cruciate ligament lies against the lateral extremity of the line and, in the fully flexed position, the posterior cruciate ligament lies against the centre and medial end.

If, however, the limb was kept for long periods in the fully flexed attitude, especially when, as must be the case in the squatting posture, there is even a strain towards further flexion, we might expect that the great pressure of the posterior cruciate ligament against the intercondylar line would make a groove in it. The medial end of the line would be so pressed up towards the popliteal surface of the bone that the line would be more convex upwards and would reach a higher level than in specimens from non-squatting people. The prominence of the intercondylar line as found in bones from modern civilised people would also be diminished owing to upward lipping or eversion of the line.

Apart, however, from the production of a visible groove on the intercondylar line it is conceivable that the pressure of the posterior cruciate liga-

ment might result in a deepening of the posterior end of the intercondylar fossa as a whole. This might especially arise if the ligament was more strongly developed and so more bulky in the squatting people than in the non-squatting. Thus in some squatting people we might find that the whole fossa would be deeper, although no actual groove was noticeable.

In fig. 1 the posterior aspect of the lower ends of two femora are shown. A is the femur of an aboriginal Australian, and B is that of a modern Irish individual taken at random from a collection kept for teaching purposes. On comparing the two bones it will be seen that, while in the Irish specimen the intercondylar line is very prominent and equally developed throughout its whole length, in the Australian the line is crossed by a shallow but distinct

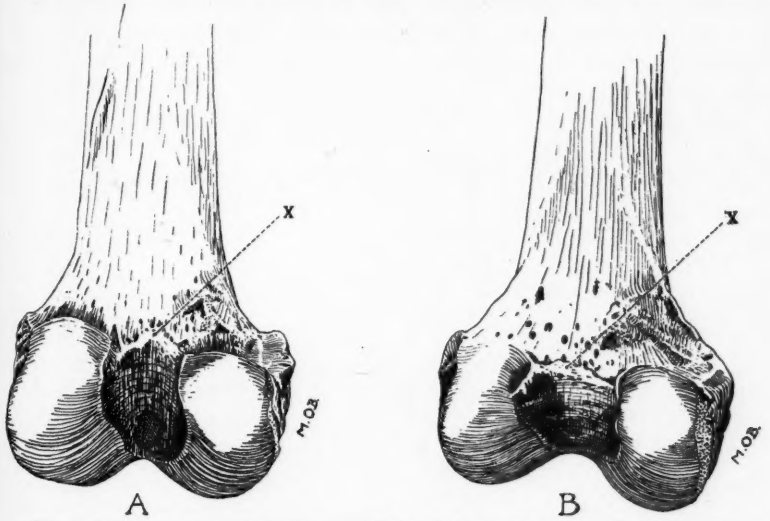

Fig. 1. Posterior aspect of two femora: A being that of an Australian aborigine, and B that of a modern Irishman. *X* marks groove for posterior cruciate ligament.

groove for the posterior cruciate ligament. This groove causes the intercondylar line to be less prominent in its medial part. The line is also everted or lipped towards the popliteal surface of the bone, and thus, being more convex upwards, it reaches to a higher level than in the Irish specimen. If a pencil is laid across the upper surface of the two condyles of this Australian bone and the bone is looked at directly from behind, it can be seen that the intercondylar line reaches as high as the pencil, while if the Irish specimen is similarly treated the line is almost half a centimetre below the pencil.

The total number of specimens examined for this feature was 169, belonging to races known to squat or in which the tibiae showed well-marked squatting facets, and 74 belonging to modern Irish or English. In the former group 110 had the groove distinct, in 22 it was poorly developed and in the

remainder it was faint or absent. In the group of modern bones, 12 had the groove definitely developed, in 9 the groove was doubtful and in the remainder it was absent.

Bearing in mind what has been already said about the possibility of some modern civilised femora approximating to those of more primitive people, these results appear to be fairly definite. With regard to the absence of a definite groove in as many as 37 out of a total of 169 primitive specimens it should perhaps be remembered that the exact degree of flexion to which the knee-joint is put by the act of squatting will vary with the obesity and muscular development of the individual. Consequently the absence of the groove in some cases may be due to the greater stoutness of the persons to whom the specimens belonged. It has also been stated that the bones described above as modern Irish are from a collection kept for teaching purposes, and, although the majority are undoubtedly correctly so described, it is quite possible that

Table I. *Showing distribution of femora according to depth of the intercondylar fossa*

	No. by which depth of fossa must be multiplied to equal antero-posterior depth of articular surface														
Group	2·7	2·8	2·9	3·0	3·1	3·2	3·3	3·4	3·5	3·6	3·7	3·8	3·9	4·0	Totals
Modern Irish	—	—	1	2	4	11	5	10	10	10	2	4	—	4	63
Modern English	—	—	—	3	—	2	3	4	—	—	—	—	—	—	12
Australian	4	4	3	16	8	4	—	1	—	—	—	—	—	—	40
Bushman	—	—	—	4	2	3	—	2	1	—	—	—	—	—	12
Andamanese	—	—	4	10	11	9	3	1	1	—	—	—	—	—	39
Early American	—	—	—	4	4	2	1	—	—	—	—	—	—	—	11
Melanesian	1	4	3	3	3	2	2	1	—	—	—	—	—	—	19
Malay	—	—	—	1	2	—	2	1	—	—	—	—	—	—	6
Polynesian	—	3	4	2	2	1	—	—	—	—	—	—	—	—	12
Veddah	—	—	—	2	—	—	2	—	—	—	—	—	—	—	4
Burmese	—	—	—	—	1	1	3	—	1	—	—	—	—	—	6
African	—	—	—	2	2	—	2	3	1	—	—	—	—	—	10
Early Irish	—	—	1	3	1	3	—	1	—	—	—	—	—	—	9

an occasional specimen from some other source may be included in the collection. Hence, possibly, the presence of the groove in some of these specimens.

To test the accuracy of the other suggestion given above, namely, that the pressure of the posterior cruciate ligament in the squatting posture might bring about a deepening of the whole intercondylar fossa in primitive people, the following measurements were carried out. The bones were laid on a plane surface with the back of both condyles and the back of the great trochanter resting on this plane. Through a small hole bored in the plane a probe was passed up till it touched the highest point on the intercondylar line. The height of the top of the probe above the plane was measured and also the greatest depth of the articular surface of the lower end of the femur in a direction vertical to the plane. Fig. 2 shows the two dimensions taken. The depth of the fossa was given by the first measurement, and this was expressed as a fraction of the depth of the articular surface. The results of these measurements in all the bones examined are given in Table I. The figures shown above the columns

are the denominators of the fractions which the depth of the intercondylar fossa made of the greatest depth of the articular surface. Thus the figure 3 means that the depth of the fossa is one-third of the depth of the articular surface.

On studying this table it will be noticed that, although there is a certain amount of overlap between the primitive and civilised groups, yet the average depth of the fossa in the two groups is very different. In the primitive group over 81 per cent. have a fossa which is deeper than 1/3·3 of the depth of the articular surface, while in the modern group a little over 31 per cent. only have

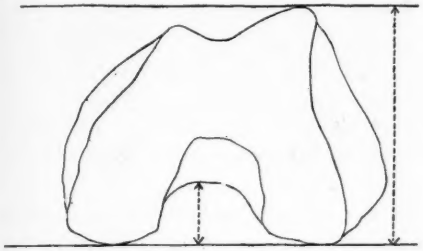

Fig. 2.

Fig. 2. Showing the measurements taken in estimating the depth of the intercondylar fossa.

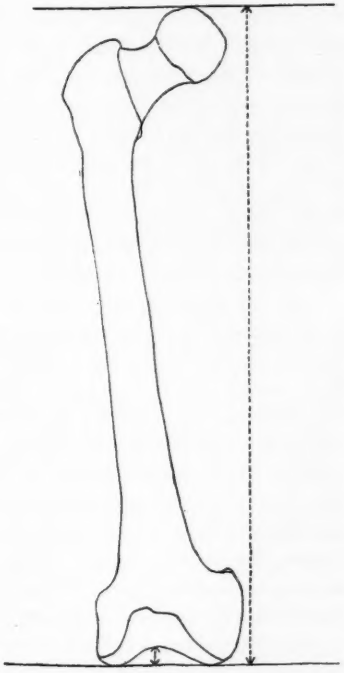

Fig. 3.

Fig. 3. Showing the measurements taken in estimating the depth of the patellar groove.

so deep a fossa. Consequently in the primitive races four out of every five femora have a fossa which is deeper than this figure, but in civilised races it is a two-to one probability that the fossa will be shallower. The table also shows that in general the depth of the fossa in the several races which make up the primitive group is very similar. The only two cases in which a majority of the specimens had a fossa which was shallower than 1/3·3 of the depth of the articular surface were the Burmese and the African. Four of the tibiae associated with the Burmese femora showed no squatting facet, and in the case of the African skeletons some were from unknown sources with no history, and

the tibiae showed doubtful squatting facets. Moreover, in both these cases the number of specimens available for examination was very small. When these facts are taken into account the difference between the primitive and civilised groups is very striking. The modern English series does not quite agree with the modern Irish, but this I think is probably due to the very small number of English bones available for measurement.

In some cases great depth of the fossa was combined with a very visible groove crossing the intercondylar line. Thus, in the collections in the Museum of the Royal College of Surgeons, I would like to refer to the specimens numbered 765 B as types in which the two features were combined. In these bones the groove was well developed and the depth of the fossa was more than a third of the depth of the articular surface. These were from a native of the Chatham Islands. This coincidence of the two features, however, was by no means a general rule. Sometimes when the groove was very visible the depth of the fossa was only moderate, as in No. 1480 (red numbers) in the Museum of the Royal College of Surgeons. This specimen is from a female Andaman Islander. The groove is very clearly shown, but the depth of the fossa is only 1/3·4 of the depth of the articular surface. Generally when the fossa was very shallow the groove was not noticeable. I was unable to determine any sex factor in the distribution of these features.

So far it has been assumed that the greater depth of the intercondylar fossa in primitive femora as compared with that found in civilised specimens is due to pressure of the posterior cruciate ligament while the limb was in the squatting posture. But two other possible causes may suggest themselves. First, the total antero-posterior depth of the articular surface may be reduced in primitive femora, thus making the depth of the intercondylar fossa relatively greater; or secondly, the greater relative depth of the fossa in primitive bones may be due to a greater projection backwards of the condyles. The first of these possibilities may be dismissed. No sign could be obtained that in primitive femora the articular surface projected forwards in front of the shaft of the bone to a less extent than in civilised ones, and if the loss of the articular surface in depth was due to a diminished backward development of the condyles, the depth of the fossa would also have been reduced. The second possibility may have some existence in fact. But an examination of these femora with deep intercondylar fossae will show that the floor of the fossa in these cases is definitely deepened, even when we take as a reference plane, not the posterior ends of the condyles, but the popliteal surface of the bone. It appears therefore that an actual deepening of the fossa by pressure of the posterior cruciate ligament is the only explanation.

THE POSTERIOR END OF THE PATELLAR GROOVE

Another feature which received attention was the patellar groove, and the possibility of variations arising in it owing to the considerable difference in general activity existing between civilised and primitive races. It seems certain

that, notwithstanding the present craze for sports of all kinds, our habits of life under modern civilised conditions are, on the whole, less active than either those of our primitive ancestors or those of existing primitive races who live by hunting. In particular the squatting attitude, generally used by primitive people, must have led to a greater use being made of the patellar groove. For in assuming this attitude and standing up again the patella is made to slide backwards and forwards in the groove to a much greater extent than in the modern motions of sitting down and standing up. Therefore it seemed quite possible that the groove in primitive femora would differ slightly from that in a modern civilised specimen.

To test this supposition the depth of the posterior end of the groove immediately in front of the intercondylar notch was measured as follows: the bones were laid as before with the back of the two condyles and the great

Table II. *Showing numbers of femora in each group in which the depth of the patellar groove was more than* 1/45 *or less than* 1/60 *of the total length of the femur*

Group	Total No. examined	No. less than 1/60	No. more than 1/45	Percentage: Less than 1/60	Percentage: More than 1/45
Modern Irish	63	5	1	7	3
Modern English	10	0	1		
Australian	36	2	4		
Bushman	9	1	0		
Andamanese	44	3	5		
Early American	11	0	0		
Melanesian	17	0	2	5	12
Malay	6	0	2		
Polynesian	12	0	1		
Veddah	4	0	0		
Burmese	6	0	0		
African	10	2	5		

trochanter resting on a plane surface. Another plane, vertical to the first, was adjusted to the inferior ends of the condyles, and the depth of the groove from the second plane was taken. This was generally done by making a true outline of the lower end of the femur while it was resting on the first plane, the outline being taken by means of a projection apparatus. Fig. 3 shows one of the outlines thus obtained. The depth of the groove was then measured on this tracing. In other cases the depth of the groove from the second plane was measured directly by means of a set square, one side of which was marked in millimetres. Both methods gave the same results, but the latter was somewhat quicker to apply. The length of the femur was also measured, not the maximum length, but the actual length with the two condyles resting on a plane at right angles to the line of measurement.

The results of these measurements are set out in Tables II and III. The depth of the groove was expressed as a fraction of the length of the femur. In the great majority of cases the depth of the groove was somewhere between 1/45 and 1/60 of the length of the femur, while a few extended above and below these limits. In Table II, the number of specimens in each racial collection

which were examined are shown and also the number of specimens in each collection in which the depth of the patellar groove transgressed the dimensions given above. It will be noticed that in the modern group, comprising both Irish and English specimens, 7 per cent. had a groove which was less deep than 1/60 of the length of the femur, while only 3 per cent. had a groove which was deeper than 1/45 of the femoral length. Turning to the primitive group, consisting of all the other specimens, we find that 5 per cent. only have a groove shallower than 1/60, while 12 per cent. have a groove that is deeper than 1/45 of the femoral length. It appears therefore that in primitive femora extreme depth of the posterior end of the patellar groove is a good deal commoner than in modern ones, but in modern civilised femora extreme shallowness of this part of the groove is somewhat commoner than in primitive ones.

Table III. *Showing distribution of all femora examined according to the depth of the patellar groove*

Group	No. examined	(A) total no. and (B) percentage of cases in which groove was more than 1/52 of length of femur	(A) total no. and (B) percentage of cases in which groove was less than 1/51 of length of femur
Modern Irish	63	(A) 31, (B) 50	(A) 32, (B) 50
Modern English	10	(A) 3, (B) 30	(A) 7, (B) 70
Early Irish	7	(A) 4, (B) 57	(A) 3, (B) 43
Australian	36	(A) 18, (B) 50	(A) 18, (B) 50
Bushman	9	(A) 7, (B) 78	(A) 2, (B) 22
Andamanese	44	(A) 26, (B) 59	(A) 18, (B) 41
Early American	11	(A) 5, (B) 45	(A) 6, (B) 55
Melanesian	17	(A) 7, (B) 41	(A) 10, (B) 59
Malay	6	(A) 6, (B) 100	(A) 0, (B) 0
Polynesian	12	(A) 5, (B) 42	(A) 7, (B) 58
Veddah	4	(A) 4, (B) 100	(A) 0, (B) 0
Burmese	6	(A) 5, (B) 83	(A) 1, (B) 17
African	10	(A) 6, (B) 60	(A) 4, (B) 40
Totals			
Modern group	73	(A) 34, (B) 47	(A) 39, (B) 53
Early and primitive group	162	(A) 93, (B) 57	(A) 69, (B) 43

When we study the separate collections from particular races which make up the two groups we meet with some apparent exceptions. The modern English collection had no instance of a groove less than 1/60 of the length of the femur, and the Bushman collection had one femur with a groove shallower than this figure but none with a groove that was deeper than 1/45. These anomalous results I ascribe solely to the smallness of the series available for examination in both these collections.

In Table III I have shown the distribution, according to the depth of the patellar groove, of all the femora examined. I have arbitrarily taken the division between 1/51 and 1/52 of the length of the femur as a line of separation, these dimensions being selected as in the modern Irish specimens practically the same number of bones fall on each side of the division. In column 3 of the table the number in each race in which the groove was deeper than 1/52 of the length of the femur are shown, and in column 4 the number in which the groove

was shallower than 1/51 of the femoral length. In the modern Irish collection practically the same number of specimens fall in each column. In the modern English collection more than twice as many fall in the shallower column as in the deeper one. When we come to the primitive races, however, we find that in most instances the majority fall on the deeper side, but in one case, the Australians, the numbers on either side were equal, and in three cases, the early American, the Polynesian and the Melanesian, the majority fall on the shallower side. Taking all the specimens as falling into two groups, namely, primitive and civilised, we find that in the civilised group a small majority of the bones is on the shallower side of the division, but in the primitive group a large majority is on the deeper side. These facts seem to indicate that the posterior end of the patellar groove is, on an average, deeper in the femora of primitive people than it is in those of civilised races. But it should be noted that the depth of the groove in some modern femora is quite as great as it is in any primitive specimen. Before leaving these tables attention may be drawn to the fact that the two collections which in Table II formed exceptions to the rule, viz. the modern English and the Bushman, in Table III, conform very well to the other collections. This rather confirms the suspicion that the figures for these two collections in Table II should be regarded as exceptional and due only to the smallness of the numbers examined.

In trying to account for this fact of the greater depth of the patellar groove in the femora of primitive people it may seem at first sight that the frequent use of the squatting position is an adequate cause. But on examining individual bones we find that great depth of the intercondylar fossa and the other features which have been already ascribed in this paper to the use of the squatting posture are often not accompanied by great depth of the patellar groove. For example, in the collections in the Museum of the Royal College of Surgeons, No. 796, a Maori from North Island had an intercondylar fossa with a depth of more than a third of the depth of the articular surface, but its patellar groove was only 1/55 of the length of the femur; and again No. 1623 (red numbers) from a Hottentot had a deep intercondylar fossa but a very shallow patellar groove. A native of Madras among the Trinity College specimens was exactly similar. If one of these features is due to the squatting attitude it seems obvious that the other is not. Reasons, that seem satisfactory, have already been given for attributing the deepening of the fossa to the squatting habit, so we must seek elsewhere for a cause for the deep patellar groove.

Probably this deepening of the patellar groove in primitive people is caused by their more active habit of life. This suggestion would also account for the fact that, although the average depth of the groove is less in civilised than in primitive people, still in a few specimens from civilised races the depth of the groove is as great as in any primitive femur. For some individuals in civilised races lead lives as active as any savage, although the average civilised individual is decidedly less active. Hence, among femora from modern civilised

races we meet with a greater range of variation in the depth of the groove. For all members of savage tribes are compelled by their mode of life to be fairly active, but members of civilised communities may be very active, but are often very sedentary. Further, in this respect, it is remarkable that two of the racial collections which gave anomalous figures in Table III are from island populations whose activities would be mostly confined to fishing and boating, and who, presumably, would have little call for great exertions on land.

If this suggestion is correct we might expect to find a sexual difference in the depth of the groove, for in practically all communities the women are less active than the men. Unfortunately, in the case of the modern Irish specimens, no record of the sex is available, and in the other racial collections the only one in which the bones were almost equally distributed between the sexes was the Andamanese, in which, as regards the collection in the Museum of the Royal College of Surgeons, there were 18 male femora and 19 female. Here the female femora did in fact show a shallower groove than the male, for instance there were four male bones with a groove deeper than 1/47 of the length of the femur but no female specimen. At the other end of the scale there were two female bones with a shallower groove than 1/60 of the length of the femur, but only one male bone had a groove shallower than this figure, and in it the groove was deeper than in the two female specimens. In all the other racial collections either one sex preponderated heavily or the sex was not recorded.

Another point observed was that the depth of the groove often differed considerably in the two limbs of the same individual. Taking all the bones together there were 59 skeletons in which both femora were present and available for comparison. In all other cases either one femur was missing or the specimens were in collections of individual bones in which the members of particular skeletons could not be identified. In the 59 complete skeletons there were 31 cases in which the groove was deeper in the right femur, 22 cases in which it was deeper in the left, and 6 cases in which the groove was equal in both limbs. These figures refer to the fraction which the depth of the groove formed of the length of the femur, and not to the absolute depth of the groove. As most people use one limb rather more than the other, if the depth of the patellar groove varies with the activity of the individual, we would expect that there might be a difference in the groove between the two limbs.

It seems therefore very probable that the diminished depth of the patellar groove in civilised races is due to a less active manner of life, but the question of a difference in the groove between the sexes requires more extended examination. Before leaving this subject I would like to point out that it is impossible that the differences shown in Tables II and III are due to a sex factor, for, although in the majority of bones from primitive people the sex was not recorded, yet it was obvious that in these the male sex preponderated, and, in the case of the specimens from individuals in which the sex had been recorded, there were ten more males than females. Likewise of the modern femora the majority were obviously from males.

THE PRESENCE OF A FACET ON THE LATERAL ASPECT OF THE LOWER END OF THE FEMUR

Returning again to an examination of a freshly dissected knee-joint. If we place it in the fully flexed position and examine it from the front with the tendon of the quadriceps femoris muscle *in situ*, it can be noticed that the central part of the tendon of this muscle passes over the supero-lateral margin of the patellar surface of the femur. While in this position it can be seen that if the tendon is closely applied to the femur, as it must be in the squatting attitude, a large part of the tendon is actually in contact with the lateral side of the femur close to the margin of the patellar surface. In moving from the extended to the flexed position it may be noticed that the patella itself moves slightly laterally, and this helps to carry part of the tendon over the lateral edge of the patellar surface. If now we examine a large number of femora it will be found that in the majority of those from modern civilised races the patellar surface has a sharp lateral edge with no evidence of an extension of the articular surface on to the lateral side of the bone, or, at most, to a very slight extent. In a minority of the specimens from civilised races, however, it will be found that this lateral edge of the patellar surface, instead of being sharp, is rounded, and the articular surface is carried so far round to the lateral aspect of the bone, that, if the femur be regarded from the lateral side, a crescentic-shaped articular facet can be seen extending from the supero-lateral angle of the patellar surface to the groove for the popliteus muscle. This lateral facet must, I think, be attributed to the tendon of the quadriceps femoris muscle playing on this area while the joint is in the fully flexed position. We therefore might expect to meet with it in the femora of squatting people.

In fig. 4 I have depicted the anterior aspects of the same femora as were shown in fig. 1, A again being the Australian and B the modern Irish specimen. In the Australian specimen the rounding of the lateral margin of the patellar surface is very marked, and, consequently, there is a very considerable facet visible from the lateral aspect of the bone. In this case the lateral facet referred to above was actually continuous with another facet further back which is due to the tendon of the popliteus muscle rubbing against the lateral edge of the condyle. This latter popliteus facet is usually present to a greater or less extent in all femora. In most cases the lateral quadriceps facet, when present, is not as large as in the femur selected for illustration, but remains separate from the popliteus facet.

In examining a large number of femora from primitive people for this feature, however, the results were very confusing. Sometimes it was very well developed, as in the Australian specimen which is shown in fig. 4. In other cases it was present but not nearly so well marked. While, on the other hand, it was absent, or only present to a very slight degree, in many femora from undoubted squatters. Moreover, it is quite well developed in many bones from

modern civilised races where we have no reason to believe that the individuals, from whom the bones came, ever made use of the squatting posture. Possibly a kneeling attitude, as well as a squatting one, may produce this facet, but, even so, we would expect to find it in the bones of all undoubted squatters. I am unable to account for these facts. The only definite conclusion that I arrived at was that the facet when present in femora of primitive squatting people, is developed to a much greater extent than it ever is in the bones of modern civilised people. Its absence from the bones of many squatters is a fact that I cannot explain.

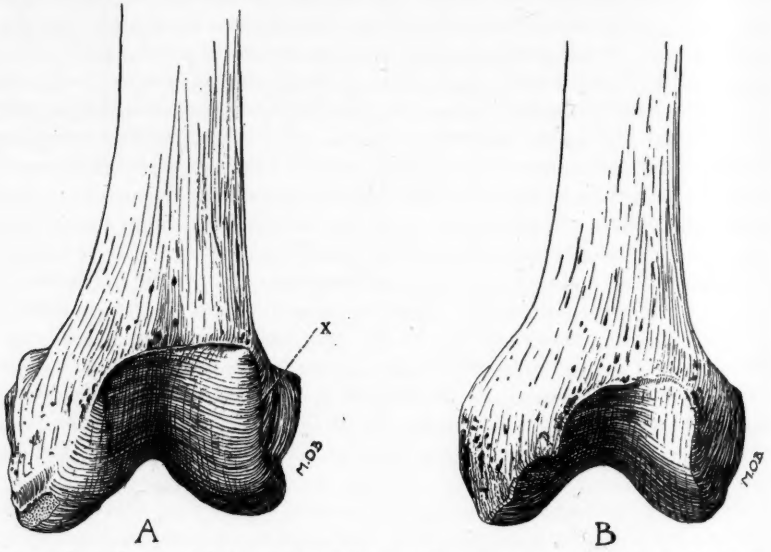

Fig. 4. View of antero-inferior surface of the same femora as are shown in fig. 1, A being the Australian and B the Irish. *X* marks the facet on lateral edge of patellar surface.

Finally, attention may be drawn to the very noticeable development of the adductor tubercle in the femora of primitive people. This may be only an indication of greater general muscular development, but, more likely, it is connected with a greater development of the adductor magnus muscle which probably is utilised, in the squatting attitude, to give stability to the limb.

CONCLUSIONS

1. In the femora of squatting people the intercondylar line is, in the majority of cases, crossed by a distinct groove for the posterior cruciate ligament. This results in the line being more convex upwards and reaching to a higher level than in the bones of civilised people. The depth of the intercondylar fossa is greater in the femora of squatters than it is in those of

civilised people. Both these facts appear to be due to pressure by the posterior cruciate ligament while the joint is fully flexed as in squatting.

2. In the femora of modern civilised races the depth of the posterior end of the patellar groove is slightly less than in the bones of primitive people. This fact does not seem to have any connection with the use of the squatting posture, but, probably, is to be accounted for by the less active habit of life followed under civilised conditions.

3. In a great number of femora belonging to squatting people the lateral edge of the patellar surface is rounded, and the articular surface is carried round on to the lateral side of the bone as a crescentic-shaped facet. This, apparently, arises from the fact that, when the knee-joint is fully flexed, the tendon of the quadriceps femoris lies over the lateral side of the patellar surface of the femur. The facet is, however, absent from the bones of many squatters, and, since it is also found in some femora from civilised races, its occurrence requires further investigation.

I am greatly indebted to Miss M. O'Brien of the Zoology Department, Trinity College, Dublin, for drawing the illustrations, and to Prof. A. F. Dixon for reading and correcting the rough draft of this paper.

REFERENCE

(1) Havelock Charles (Oct. 1893). *J. Anat. and Phys.* vol. xxviii, p. 10.

A NOTE ON THE IDENTIFICATION OF THE LUMBAR VERTEBRAE OF MAN

By EDWARD FAWCETT

Various editions of textbooks appear, some of which inform us how it is possible to identify individual vertebrae, and I have no doubt that they mostly agree in the number of the individual vertebrae of the various subdivisions of the vertebral column which it is possible to identify, so that point does not need labouring. But when they stress the point—not directly but by implication—that the fifth lumbar vertebra is the only one of the lumbar series that can be recognised, I think it is time, in modern language, to "butt in."

Everyone soon learns that the number of lumbar vertebrae is variable, varying from four to six, but as these variations are not very common they need not necessarily upset the statements about to be made. In any event, the statements are made more with the view of exciting interest in the matter and obtaining information than for any other reason. I hope that, if they are not warranted by the consensus of experience, such experience will be forthcoming as "evidence against." In order to make a start, I will quote verbatim the remarks concerning the fifth lumbar vertebra, which from some textbooks seems the only one which can be identified:

"The distinctive characters of this vertebra are as follows: (1) It is the most massive of all the lumbar vertebrae. (2) The greater depth of the body in front is more conspicuous than in the others. (3) The transverse processes are massive, conical and directed definitely upwards. (4) The inferior articular processes are wide apart."

This is followed by the statement that "It will be readily understood that attempts at all these characteristics may occur in the fourth lumbar vertebra though the marked increase in depth of the anterior surface of the body on the fifth is seldom reached in the fourth."

From another quotation it can be directly inferred that the fifth alone is capable of identification, for the statement is "the fifth lumbar vertebra has distinguishing features of its own; the others belong to a common type."

No quotation could be complete if it left out the account given in Macalister's textbook, as everyone who knew him was aware that but little escaped him concerning the bones that make up the skeleton. He says:

"Each of the five lumbar vertebrae exhibits gradational peculiarities. The first has the most distinct transverse processes and tuberosity [by transverse processes Macalister means 'accessory' processes], the smallest costal process and the narrowest pedicle. The fifth is a passage vertebra with a wedge-shaped

body, a thick rough costal process, widely divaricated inferior articular processes (nearly as far as the superior) and a smaller round-edged spine. The second, third, and fourth can be distinguished by the gradually widening pedicles, the diminishing mammillary processes and the increase in body-width and divarication of the lower articular surfaces."

Such a description is well enough if one has all the lumbar vertebrae to hand: it is useless so far as concerns any individual vertebra, and, if it be possible to be reasonably accurate, then we may as well be so.

If two vertical parallel wires be run down the centre of the lumbar vertebrae to hold them firmly in position and if they be reasonably separated from

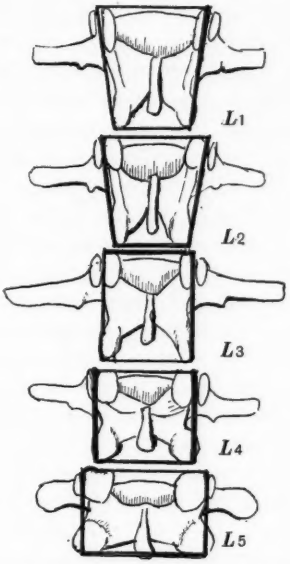

Fig. 1. The lumbar vertebrae seen from behind.

one another so that they do not overlap, it will be noticed, as is said in most of the textbooks, that the distance between the upper and lower articular processes is greater in the first, second and third vertebrae than in the fourth and fifth. It will be further noticed that the upper articular processes are wider apart than the lower ones in the first and second vertebrae, that they are about equidistant in the third and fourth, but in the fifth the lower articular processes may be even wider apart than the upper ones.

It is possible to construct angular figures whose angles will sufficiently accurately contain the articular processes and these figures are such that our task of identification is rendered very easy as a rule: thus a figure such as is rendered in fig. 1 *L*1, which is a trapezium, will contain in its angles the

articular processes of the first and second vertebrae. A figure which is a parallelogram with long vertical sides will contain in its angles the articular processes of the third lumbar vertebra, fig. 1 *L*3. As is well known too the costal process of the third is very long, so that should there be a doubt the presence of an obviously very long costal process should be enough to dispel it.

The articular processes of the fourth can be got into the angles of a square figure and even if not exactly containable in a square there is a squareness about the appearance which is unmistakable, fig. 1 *L*4. In the case of the fifth, the articular processes may be fitted with sufficient accuracy into the angles of a parallelogram whose long sides are the horizontal ones, fig. 1 *L*5. This is by far the best method of recognising the fifth vertebra.

Now it sometimes happens that a vertebra is met with which resembles a last lumbar vertebra but perhaps on one side has an enormously developed costo-transverse process. It will be found that the upper articular processes are wider apart than the lower ones and in most cases the spinous process is vertically cleft showing that the two halves have not united. Such a vertebra is an ununited first sacral one and would lie in the angles of a very squat trapezium whose upper side is longest.

It has been said above that a trapezial figure will contain the articular processes of the first and second lumbar vertebrae: that being so, how are we to distinguish between the two? Here I must confess a difficulty. In the specimens I have I cannot find any character so striking to the eye that is possessed by one and not by the other; but I find that the vertical height of the back of the centrum of the first vertebra when measured by calipers is greater than that of the front of the centrum, whilst the two heights are equal in the second vertebra. This difference can only be made out with the calipers and I fancy in certain races may not exist.

To sum up we may say that in the first and second lumbar vertebrae the articular processes will lie in the angles of a trapezium whose long axis is vertical.

In the third these processes will lie in the angles of a parallelogram whose long sides are vertical and the costal processes are obviously very long as a rule.

In the fourth the articular processes lie in a square or "squarish" figure.

In the fifth these processes lie in the angles of a parallelogram whose long sides are horizontal: frequently the lower articular processes are wider apart than the upper.

THE VASCULAR SUPPLY OF THE PITUITARY BODY IN THE DOG[1]

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The earliest description of the blood supply of the pituitary gland was given by Duret (1872) in his classical work upon the blood supply of the brain, in which he makes reference to a small bilateral branch of the posterior communicating artery of the circle of Willis, passing to the infundibulum.

It was not until 1908, however, that Herring (10), using a carmine gelatin injection mass, showed that the anterior and posterior lobes of the pituitary gland were supplied by branches of the circle of Willis, which were quite distinct from each other, the vessels to the anterior lobe passing down the stalk, whilst those to the posterior lobe entered it directly.

A more detailed account of the blood supply to the pituitary gland was given by Dandy and Goetsch (5). These workers showed that in the dog, the anterior lobe receives its arterial blood supply from 18 to 20 arterioles, arising from the circle of Willis (i.e. 8–10 from the anterior communicating artery, 3–5 from the posterior communicating artery, and a pair on each side from the internal carotid artery). These vessels run towards the stalk of the gland and enter the anterior lobe near its attachment. In the substance of the pars anterior, they form sinus-like channels, lined by a simple layer of endothelium, which is directly in contact with the cells of the anterior lobe. From these sinuses, the blood is drained back into the basilar circle of veins which overlies the circle of Willis. The pars intermedia, as described by Dandy and Goetsch (5), consists of two parts. Of these, according to these workers, the part which we now call the pars tuberalis receives its blood supply from the stalk and from the pars anterior. The pars intermedia proper—that part forming an epithelial investment to the pars nervosa—is, on the other hand, entirely devoid of vessels. The posterior lobe (pars nervosa) is supplied by a median vessel formed by the union of a small branch from the internal carotid arteries on either side. The blood from this region is collected into the basilar veins of the circle of Willis.

During the last few months, Popa and Fielding (14) have shown in the human pituitary that the blood from the anterior and posterior lobes is not entirely drained into the circle of Willis, but that a considerable amount of it passes up through a number of parallel veins into the tuber cinereum. These

[1] Part of thesis approved for the degree of Ph.D. in the University of London.

Page 387, 6th line from bottom, for the first "of" substitute "accompanying", also on p. 396, 3rd line from top.

vessels ramify in relation to the nuclei of this region, and have been called "hypophysio-portal veins."

METHOD OF INJECTION

Dogs were used for this investigation and were injected with carmine as follows. The dog was anaesthetised with chloroform and was bled through a canula tied into one of the carotid arteries. The common carotids were then ligatured caudally and canulae were tied into each of them pointing cranially. Similarly both the jugular veins were ligatured and canulae were tied into each of them, also pointing cranially. The arterial canulae were then connected to a warm saline reservoir by means of a Y-shaped tube, whilst the venous canulae were similarly connected to a rubber tube and formed an outlet for the perfusing fluid.

The animal was perfused with a 0·9 per cent. saline solution, containing 0·001 per cent. sodium nitrite, which latter substance acted as a capillary dilator and ensured a good capillary injection with the carmine gelatin. The saline was kept at a temperature of 36–40° C. and injected at a pressure of about 125 mm. of mercury, whilst to avoid any oedema of the tissues, the perfusion was stopped before the blood was completely removed from the animals.

Carmine gelatin was then injected into the carotids by means of a special syringe (see text-fig. 1) carrying two nozzles, *a* and *b*. The nozzle *a* was connected to the arterial canulae and *b* to a rubber tube, which was immersed in the carmine gelatin mass kept at 40° C. When the injection was deemed complete, the jugular veins and the carotid arteries were ligatured and the animal was placed in the ice chamber over-night, to allow the carmine to set. The following day the pituitary, along with a part of tuber cinereum, was dissected out, and fixed in 10 per cent. formalin.

In some cases, the perfusion was carried through one of the carotids, the other being ligatured off. In such cases the jugular vein of the same side was ligatured as low as possible and that of the opposite side was used as an outlet. This also gave excellent results.

Indian-ink injections of various dilutions were tried, but the results were not satisfactory, whilst attempts to inject through the jugular veins with a carmine gelatin mass were not successful.

After fixation in 10 per cent. formol, the material was cleared in cedarwood oil and embedded in paraffin. Sagittal and coronal serial sections were cut, about 20 μ in thickness and were counter-stained with Ehrlich's or Weigert's haematoxylin.

Reconstructions were made of the blood vessels in the injected specimens by means of the tracing-paper method.

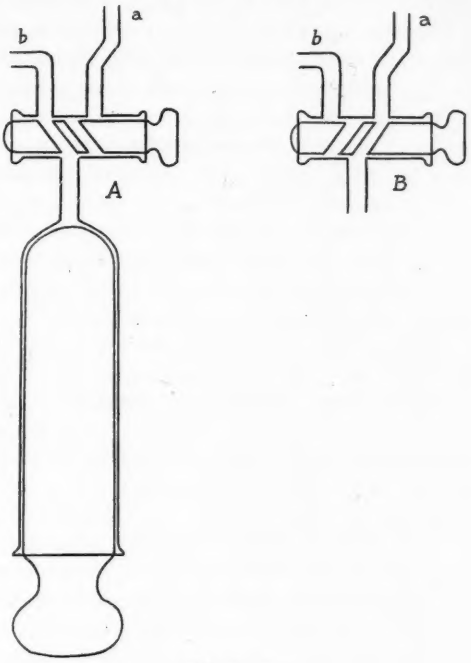
OBSERVATIONS

The pituitary body lies surrounded by the circle of Willis, from which numerous vessels converge towards the gland. The stalk in the dog is ex-

tremely short, so that the vessels appear to run towards it. Round this region they are distributed to the pars anterior, pars tuberalis and pars nervosa.

(1) *Vessels of the pars anterior* (text-fig. 2, *A*.)

The pars anterior is supplied with blood from branches of the circle of Willis (text-fig. 2, *a*.). These vessels chiefly enter the pars anterior in the region of the stalk, and among the glandular cells they break up into large irregular anastomosing sinusoids (text-fig. 2, *bl.s*.). These channels are lined by a single layer of endothelium, which is directly in contact with the cells of the anterior



Text-fig. 1.

lobe. Some of the blood from the sinusoids passes back into the venules of the basilar circle of Willis, but the greater part passes into the pars tuberalis (text-fig. 2, *T*.) through the anastomosis of the vessels of this region with those of the pars anterior.

(2) *Vessels of the pars tuberalis* (text-fig. 2, *T*.)

The pars tuberalis derives its blood supply from the branches of the circle of Willis (text-fig. 2, *a*.) as well as from the sinuses (*bl.s*.) of the pars anterior. In this region there is developed a rich sinusoidal network (text-fig. 2, *bl.s.T*.)

Page 389, 6th line from bottom, and *page* 392, 4th line,

into which the sinusoids of the pars anterior open. From this sinusoidal network (*bl.s.T.*) the greater part of the blood passes into the vessels of the stalk (*c.arc.T.*) and from there reaches the tuber cinereum. Other vessels ($hp.v._2$) run directly to the tuber cinereum, to the pars nervosa (*c.n.*) and to the basilar venous circle [redacted]

(3) *Vessels of the pars nervosa* (text-fig. 2, *N.*)

The pars nervosa is less vascular than the pars anterior and pars tuberalis and is supplied by blood from the sinuses of the pars tuberalis (*bl.s.T.*) and from the posterior lobe artery (text-fig. 2, *p.l.a.*). This artery enters the posterior lobe at its posterior upper extremity and some of its branches run forwards towards the central cavity of the infundibular recess, whilst others form a plexus on the surface of the pars nervosa. This plexus is joined by the vessels running from the pars tuberalis (text-fig. 2, *c.n.*). The vessels from the pars tuberalis form a channel through which blood from the pars anterior is intermixed with that of the pars nervosa. This collateral circulation has already been described by Dandy and Goetsch (5).

From this plexus (text-fig. 2, *c.pl.*) capillaries (*c.*) run into the substance of the pars nervosa (*N.*), where they form a rich capillary plexus. This plexus has been described by Dandy and Goetsch (5) and Herring (10), although the vascularity of this region has not hitherto been realised. Vessels also run into the pars intermedia (text-fig. 2, *I.*) but these are few in number, for as Herring (10) has shown, the pars intermedia is the least vascular part of the pituitary body. This has recently been confirmed by Brown (1) working on the pituitary of the rat.

The larger blood vessels of this plexus, when they penetrate into the substance of the pars nervosa are frequently accompanied by prolongations of the epithelial cells of the pars intermedia, which form a sheath to the vessels (Plate I, fig. IV, *c.sh.*). Round these vessels one also finds a fibrous sheath, derived from neuroglial cells and nerve fibres. Small "hyaline bodies" are sometimes found in the perivascular sheaths. These bodies have been described by Herring (9) in the cat.

(4) *Vessels of the pituitary stalk* (text-fig. 2, *S.*)

The stalk receives its blood supply chiefly from the capillary plexus of the pars nervosa (text-fig. 2, *c.arc.*). Vessels from the sinuses of the pars tuberalis (text-fig. 2, Plate I, figs. I, II and III, *c.arc.T.*) and from the circle of Willis also ramify in this region.

The capillary plexus formed by these vessels consists of a series of arched capillaries (text-fig. 2, *c.arc.T.* and *c.arc.*) pointing towards the ependyma (text-fig. 2, *ep.*) of the infundibular recess. These arched vessels appear to be comparable to part of the "secondary net" described by Popa and Fielding (15). This condition in the dog may be due perhaps to the shortness of the stalk and

the prolongation into it of the cavity of the third ventricle, whereby these vessels come into immediate approximation with the ventricular ependyma.

The vessels which enter the stalk from the pars nervosa and pars tuberalis are often covered by an incomplete cellular sheath, derived from cells of the pars intermedia or pars tuberalis (Plate I, fig. II, *c.sh.*) and outside this is often found a condensation of neuroglial elements which constitutes a fibrous sheath. This glial sheath is found on the smallest vessels of the secondary net in the stalk, although it is absent round the vessels of this network in the tuber cinereum. Herring (10) has shown that the tissue actually surrounding the large vessels is sometimes rather looser in texture than the nervous tissue forming the main bulk of the stalk, and this I can confirm in my preparations (Plate I, fig. V, *l.m.*).

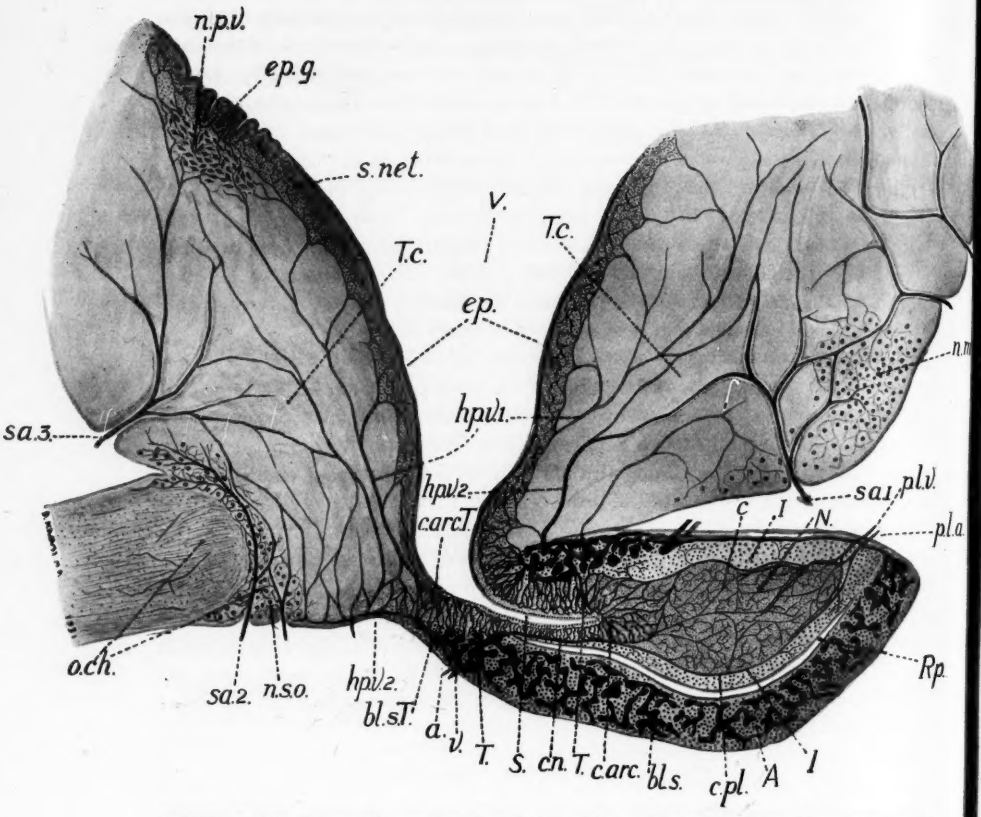
Towards the infundibular recess, some of the vessels appear to be contracted to such an extent that their lumina are scarcely visible. Dandy (6) and Croll (3) have described a rich nerve supply in these vessels.

From the "secondary net" formed in the stalk, the blood is drained into a series of vessels which constitute part of the hypophysio-portal system, and which run up into the tuber cinereum. This system has been described by Popa and Fielding (14) in the human pituitary. The hypophysio-portal vessels in the human are long, running through the stalk to the tuber cinereum and under the ependymal lining of the third ventricle they form an arched capillary plexus, the secondary net. In the dog, dependent on the shortness of the pituitary stalk and the projection of the lumen of the third ventricle into it, the vessels comparable to those in the human are extremely short and form a secondary net under the ependyma in the stalk itself. From this secondary net other long vessels of the hypophysio-portal system (text-fig. 2, $hp.v._1$) pass to the tuber cinereum. In addition, other vessels of the hypophysio-portal system ($hp.v._2$) run directly from the sinuses of the pars tuberalis to the tuber cinereum.

(5) *Vessels of the tuber cinereum*

The tuber cinereum is that part of the brain surrounding the pituitary stalk, and stretches from the optic chiasma to the mammillary bodies. It receives its blood supply partly from the systemic vessels of the circle of Willis (text-fig. 2, $s.a._1$, $s.a._2$, $s.a._3$) and partly from the "hypophysio-portal" veins ($hp.v._1$, $hp.v._2$) of the pituitary body. These latter vessels reach the tuber cinereum either from the secondary net in the stalk or directly from the pars tuberalis. I have called the vessels running through the stalk the primary hypophysio-portal veins ($hp.v._1$), to distinguish them from those passing to the tuber cinereum directly from the pars tuberalis, the secondary hypophysio-portal veins ($hp.v._2$).

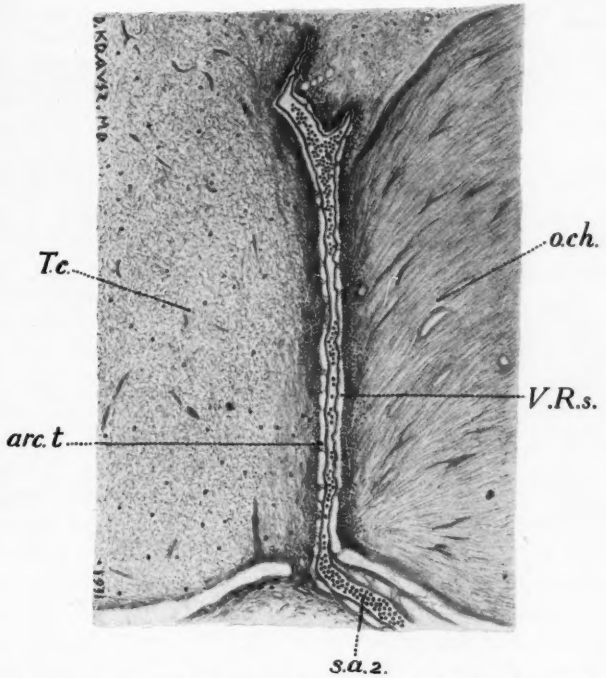
The hypophysio-portal veins, according to Popa and Fielding (15), become surrounded by thick sheaths derived from the surrounding glial tissue, so that they can be readily distinguished from the systemic vessels by the possession of this sheath. In my preparations it seemed that these vessels were not



Text-fig. 2. Diagrammatic reconstruction of the pituitary gland of the dog to show blood supply. The arteries (*a.*) from the circle of Willis which supply the pars anterior (*A.*) and the pars tuberalis (*T.*) form the blood sinuses (*bl.s.*, *bl.s.T.*) amongst the glandular cells. The blood is drained away from this region by the veins (*v.*) to the basilar circle of Willis and into the capillary plexus (*c.pl.*) of the posterior lobe. This plexus lies between the pars nervosa (*N.*) and the pars intermedia (*I.*) and receives in addition branches from the posterior lobe artery (*p.l.a.*). Capillaries (*c.*) from this plexus ramify in the pars nervosa (*N.*) and the pars intermedia (*I.*). This plexus is drained by the posterior lobe vein (*p.l.v.*), by the capillary arches (*c.arc.*) into the stalk (*S.*) and into the tuber cinereum (*T.c.*). These latter vessels, which pass from the posterior lobe to the tuber cinereum (*T.c.*) are the hypophysio-portal veins. The primary hypophysial-portal veins ($hp.v._1$) pass from the posterior lobe to the stalk (*S.*) and then to the tuber cinereum (*T.c.*), whilst the secondary hypophysio-portal veins ($hp.v._2$) run direct from the blood sinuses (*bl.s.T.*) of the pars tuberalis (*T.*) to the tuber cinereum (*T.c.*). Systemic vessels ($s.a._1$, $s.a._2$, $s.a._3$) from the circle of Willis also pass to this region. These vessels form a capillary plexus round the nuclei of the tuber cinereum (*T.c.*) and under the ependyma (*ep.*). For other reference letters see p. 398.

enclosed in a perivascular space, the so-called space of Virchow-Robin, which clearly surrounded the systemic vessels (compare text-fig. 3, *V.R.s.*, and text-fig. 4, $hp.v._1$), so that they could also be differentiated in this way.

The hypophysio-portal veins and systemic vessels are non-muscular, with the exception of the systemic arteries which have a small amount of muscle in their media. The two systems are not completely separate and the vessels

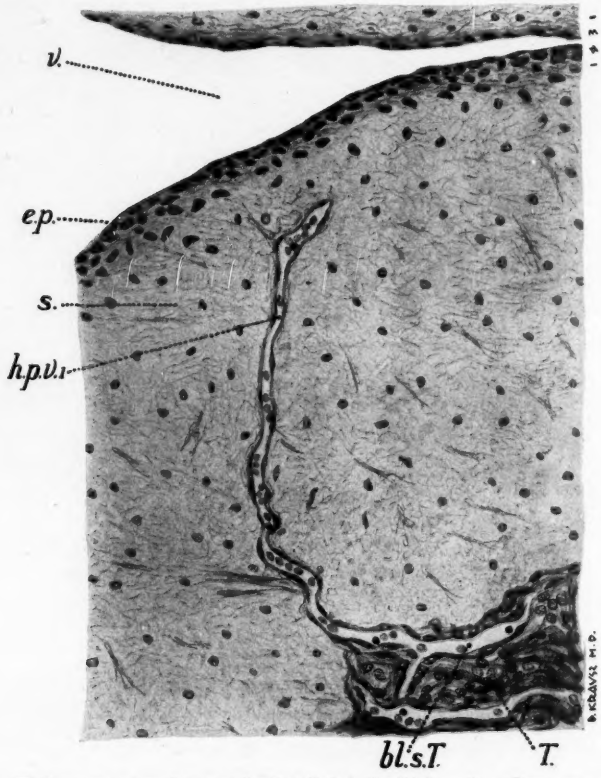


Text-fig. 3. High-power drawing of the tuber cinereum (*T.c.*) of dog. Mag. × 75 to show a systemic artery ($s.a._2$). This vessel is surrounded by a Virchow-Robin space (*V.R.s.*) whose outer wall is connected to the tunica adventitia of the artery by means of delicate bridges of arachnoidal tissue (*arc.t.*). For other reference letters see p. 398.

anastomose to some extent, especially near their entrance into the tuber cinereum.

Certain workers, Collin (4), Rasmussen (16), and more recently Popa and Fielding (15), have described colloid in the hypophysio-portal veins, but although colloid was present in my preparations of uninjected pituitary gland, among the cellular elements of the pars nervosa and tuber cinereum, I could find no trace of it in the hypophysio-portal veins. My results are therefore in agreement with those of Ch. Livon (12), Edinger (7) and Herring (9), who have failed to find it in the blood vessels.

The greater number of hypophysio-portal veins enter the tuber cinereum, anterior to the infundibular recess, and run to the various nuclei of the substantia grisea, which extends from the cephalic end of the optic chiasma to the mammillary bodies. These nuclei lie under the wall of the third ventricle and the non-medullated fibres arising from them form in the region of the stalk compact bundles which run into it, and ramify, as Greving (8) states, in



Text-fig. 4. High-power microphotograph of stalk (*s.*). Sagittal section. Dog, mag. × 209. Note the long hypophysio-portal vessel ($hp.v._1$) arising from the pars tuberalis (*T.*) and passing up through the stalk (*s.*) towards the tuber cinereum. Note the absence of the Virchow-Robin space round the vessel ($hp.v._1$). For other reference letters see p. 398.

"basket-like fashion" around the cells of pars intermedia. In naming the cell groups in the tuber cinereum I have followed Greving (8). The nucleus supra-opticus (text-fig. 2, *n.s.o.*) subdivided into a dorso-lateral, dorso-medial and a ventro-medial group of cells, lies at the cephalic end of the substantia grisea and projects into the tuber cinereum over the optic chiasma (text-fig. 2, *o.ch.*). This nucleus is mainly supplied by the secondary hypophysio-portal veins

(*hp.v.*$_2$), which enter the tuber cinereum directly from the pars tuberalis and by the systemic vessels (*s.a.*$_2$) from the circle of Willis. These vessels anastomose together and curve round the optic chiasma, forming a capillary plexus round the cells of the nucleus. A few of the primary hypophysio-portal vessels which enter the tuber cinereum from the stalk may also be traced into this plexus.

The nucleus para-ventricularis (text-fig. 2, *n.p.v.*) lies along the anterior wall of the third ventricle close to its ependymal lining and is, unlike the nucleus supra-opticus, supplied mainly by the primary hypophysio-portal vessels (*hp.v.*$_1$), though a few of the secondary hypophysio-portal vessels may be traced into it. The nucleus further receives a few branches from the systemic arterioles (text-fig. 2, *s.a.*$_3$) and a dense capillary network is formed amongst its cells.

The nucleus tubero-mammillaris is a diffuse, ill-defined mass of cells which, according to Morgan (13) extends between the optic chiasma and the mammillary bodies and lies mainly in the lateral wall of the tuber cinereum. This nucleus is mainly supplied by the primary hypophysio-portal vessels and a few systemic arterioles.

The nuclei of the mammillary body (text-fig. 2, *n.mam.*), consisting of a ventro-medial nucleus magno-cellularis and a dorso-lateral nucleus parvo-cellularis, are supplied by both the primary and secondary hypophysio-portal vessels and also by the systemic arterioles (text-fig. 2, *s.a.*$_1$). My sections did not include the nucleus para-medianus, so that I can give no account of its blood supply.

The hypophysio-portal veins form a capillary network (text-fig. 2, *s.net.*) or "secondary net" immediately under the ependyma (*ep.*), the whole structure being supported by interlacing ependymal fibres. Such a "secondary net" has been described by Popa and Fielding (15) in the human hypophysis, where the capillaries forming this network, according to them, are not covered by the glial sheaths of the larger vessels, and I can confirm their statement in the dog.

The ependymal cells, lining the infundibular recess of the floor of the third ventricle, show many variations. Kappers (11) and Charlton (2) call attention to the tubular glands formed by the modified ependymal cells, in certain regions of the brain of Fishes, Reptiles, Birds and Mammals. They also describe albumin-like substance in their lumina, which they consider to be an ingredient of the cerebro-spinal fluid.

In the dog, similar modifications of the ependymal lining occur in the region of the nucleus para-ventricularis (text-fig. 2, *n.p.v.*), where long tubular glands are formed by the ependymal cells (*ep.g.*). These are vascularised by the secondary net of capillaries which is particularly well-developed in this region.

SUMMARY

1. The pituitary gland receives its arterial blood supply from the branches of the circle of Willis and from the internal carotid arteries.

2. The vessels which supply the pars anterior enter it chiefly through the stalk and form irregular sinusoids among the glandular cells (text-fig. 2, *bl.s.*). From these sinusoids the blood is drained partly into the basilar veins (*v.*) of the circle of Willis and partly into the sinuses of the pars tuberalis (*bl.s.T.*).

3. The pars tuberalis is supplied with blood by branches of the circle of Willis, as well as by the sinuses of the pars anterior. These vessels form sinuses among the cells of the pars tuberalis and from them the blood is drained partly into the circle of Willis, partly into the stalk (text-fig. 2, *c.arc.T.*) and partly into the pars nervosa (*c.n.*). Some blood passes directly into the tuber cinereum ($hp.v._2$).

4. The pars nervosa (text-fig. 2, *N.*) receives its blood supply from the posterior lobe artery (*p.l.a.*) and from the sinuses of the pars tuberalis. These vessels form a capillary plexus (*c.pl.*) on the surface of the pars nervosa, from which vessels (*c.*) run into the substance of this region and into the pars intermedia. The vessels passing to this latter region are few in number.

5. The blood from the pars nervosa is drained partly by the posterior lobe vein (text-fig. 2, *pl.v.*) into the lateral sinus and partly into the stalk through a series of arched capillaries (*c.arc.*).

6. The blood is drained from the pars tuberalis and pars nervosa into the tuber cinereum through a series of short parallel vessels, the hypophysio-portal veins (text-fig. 2, $hp.v._1$, $hp.v._2$). The tuber cinereum receives also arterial blood directly from the systemic vessels of the circle of Willis (text-fig. 2, $s.a._1$, $s.a._2$, $s.a._3$).

7. The systemic vessels are enclosed in a perivascular space—the space of Virchow-Robin (text-fig. 3, *V.R.s.*)—which cannot be seen round the smaller systemic vessels or round the vessels of the hypophysio-portal system (text-fig. 4, $hp.v._1$).

8. The hypophysio-portal vessels supply the nuclei of the substantia grisea of the tuber cinereum. These nuclei receive arterial blood in addition from the circle of Willis.

9. The hypophysial-portal vessels also form a well-marked capillary plexus (text-fig. 2, *s.net.*) under the ependyma of the infundibular recess and also in the region of the nucleus para-ventricularis (*n.p.v.*) where the ependyma is modified into long tubular gland-like structures (*ep.g.*).

This work has been carried out in the Department of Anatomy and Embryology under the direction of Prof. J. P. Hill, F.R.S., to whom I wish to express my thanks for his help and criticism during the course of the investigation. I also wish to thank Prof. E. B. Verney for supplying me with animals and for permission to use his laboratory for the injections. I am indebted to Mr F. J. Pittock for the photomicrographs and to Dr D. Krause for the drawings of text-figs. 1–4.

Page 396, 8th line from top, for "circle of Willis" substitute "basilar veins".

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EXPLANATION OF PLATE

Fig. i. Low-power microphotograph of a sagittal section of pituitary gland. Dog. Carmine injection. Mag. × 16·5. Note the pars anterior (*A.*) and pars nervosa (*N.*). Arched capillaries (*c.arc.T.*) can be seen passing from the pars tuberalis (*T.*) into the stalk (*s.*).

Fig. ii. High-power microphotograph of part of the section shown in fig. 2. Dog. Carmine injection. Mag. × 100. Note the arched capillaries (*c.arc.T.*) passing from the blood sinuses (*bl.s.T.*) of the pars tuberalis (*T.*) into the stalk (*S.*).

Fig. iii. Low-power microphotograph of a coronal section of pituitary gland. Dog. Carmine injection. Mag. × 16. Note (1) pars anterior (*A.*), (2) pars tuberalis (*T.*), (3) stalk (*S.*), (4) tuber cinereum (*T.c.*). Arched capillaries (*c.arc.T.*) can be seen passing into the substance of the stalk from the blood-sinuses (*bl.s.T.*) of the pars tuberalis (*T.*). The primary hypophysio-portal veins ($hp.v._1$) can be seen in trans-section of the stalk (*S.*) and one in longitudinal section on the left-hand side of the third ventricle (*v.*).

Fig. iv. Low-power microphotograph of posterior lobe of pituitary gland. Dog. Carmine injection. Sagittal section. Mag. × 24. The pars nervosa (*N.*) is seen surrounded by the pars intermedia (*I.*), the cells of which form a perivascular sheath (*c.sh.*) round the vessel (*p.l.a.*) which enters the pars nervosa (*N.*).

Fig. v. High-power microphotograph of pituitary gland. Dog. Silver preparation. Mag. × 134. Sagittal section of stalk (*S.*). Note the two capillaries (*c.arc.T.*) arising from the blood sinuses (*bl.s.T.*) of the pars tuberalis (*T.*) arching into the stalk (*S.*). Note also that the matrix (*l.m.*) surrounding these vessels is looser in texture.

LIST OF ABBREVIATIONS

A.	=pars anterior.
a.	=artery.
arc.t.	=arachnoidal tissue.
bl.s.	=blood sinus of pars anterior.
bl.s.T.	=blood sinus of pars tuberalis.
c.	=capillary.
c.arc.	=capillary arches arising from vessels of pars nervosa.
c.arc.T.	=capillary arches arising from blood sinuses of pars tuberalis.
c.n.	=capillary from the blood sinuses of pars tuberalis to the capillary plexus of pars nervosa.
c.sh.	=cellular sheath for the vessels of pars nervosa and stalk.
ep.	=ependyma.
ep.g.	=ependymal gland.
h.b.	=hyaline body.
$hp.v._1$	=primary hypophysio-portal vessel.
$hp.v._2$	=secondary hypophysio-portal vessel.
I.	=pars intermedia.
l.m.	=loose matrix.
N.	=pars nervosa.
n.p.v.	=nucleus para-ventricularis.
n.s.o.	=nucleus supra-opticus.
n.mam.	=nucleus mammillaris.
o.ch.	=optic chiasma.
p.l.a.	=posterior lobe artery.
p.l.v.	=posterior lobe vein.
R.p.	=Rathke's pouch.
S.	=stalk.
$s.a._1$, $s.a._2$, $s.a._3$	=systemic arterioles from the circle of Willis.
s.net.	=secondary net.
T.	=pars tuberalis.
T.c.	=tuber cinereum.
V.	=third ventricle.
v.	=vein.
V.R.s.	=Virchow-Robin space.

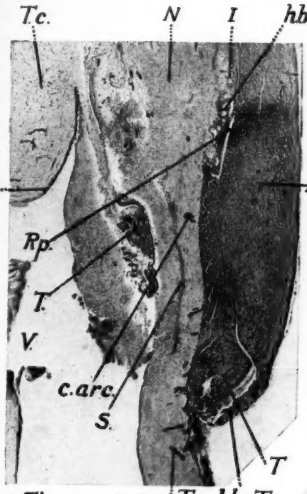

Fig. I.

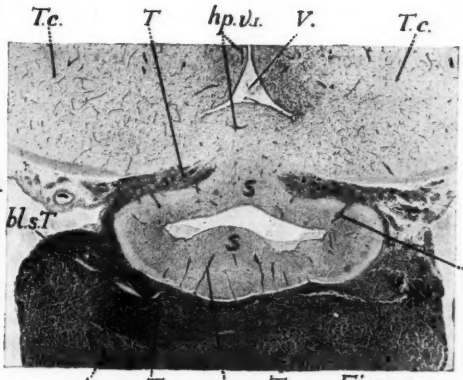

Fig. III.

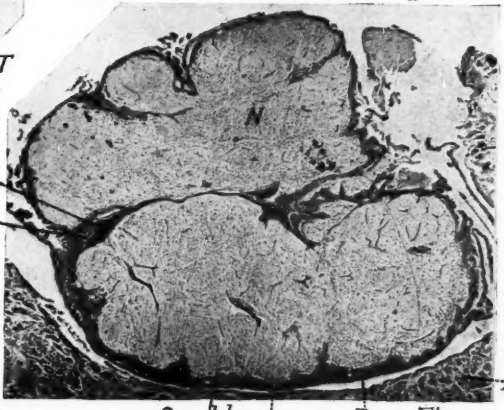

Fig. IV

Fig. II.

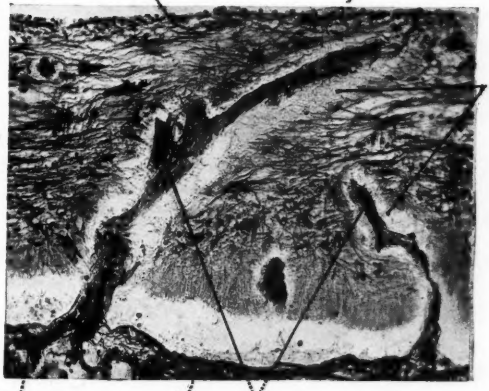

Fig. V.

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THE MORPHOLOGICAL CHARACTERS OF THE AUSTRALIAN SKULL

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INTRODUCTION

The cranial material forming the basis of this report is housed in the Museum of the Royal College of Surgeons of England. To the Council I am indebted for access to the unsurpassed collection of human osteological material, and to Sir Arthur Keith, Conservator, and Miss Miriam L. Tildesley, Research Assistant, for an untiring interest and constant co-operation. The material was studied while I was a United States National Research Council Fellow in Physical Anthropology, 1930–31.

During the course of a biometric and craniostatic analysis of the adult Australian skull, and a detailed study of the skull of Australian children, I had occasion to note the various morphological phenomena in an attempt to interpret their significance first as racial criteria, secondly as a possible indicator of the several growth phases I had established. It was, therefore, with great interest that I read the illuminating series of papers on a similar subject by Frederic Wood-Jones, dealing with the Hawaiian skull and the skull of the prehistoric inhabitants of Guam[1]. The present paper adds to the series and in its treatment maintains, in the interests of comparability, much the same sequence in the recording of observations.

In all, 113 male skulls and 70 female skulls were studied, divided geographically as follows:

	Male	Female
Northern Territory	6	2
Queensland	21	8
Western Australia	8	4
Southern Australia	28	27
New South Wales	14	10
Victoria	24	11
Unclassified	12	8
Total	113	70

Only those skulls were accepted which were definitely aboriginal, so far as the Museum records went, and, as the study progressed, experience dictated. Where there was any doubt the skull was not included. Finally, owing to the fact that some of the skulls were imperfect, not all of the observations could be made on any one skull. I have, therefore, indicated for each morphological feature the number of skulls available for the specific trait. The material is grouped as a whole, for the number available for any given geographical region is too small to give significant results when treated separately.

[1] See *J. Anat.* vol. LXV, pt. 2, pp. 179–98; pt. 3, pp. 368–79; and pt. 4, pp. 438–46.

Figs. 1–4. Male Australian from Northern Territory. R.C.S. 20. 1701.

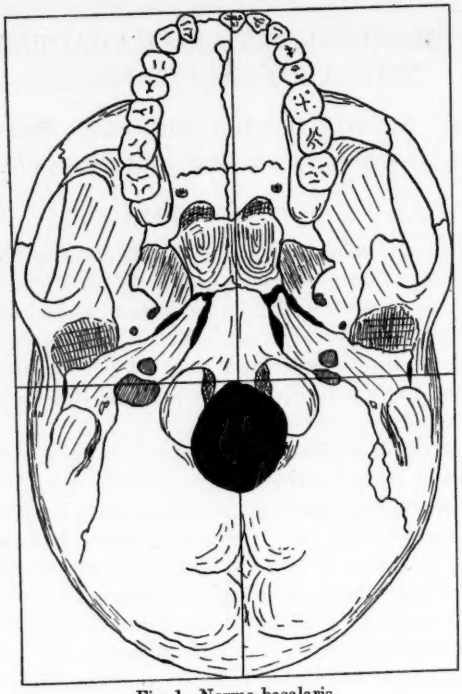

Fig. 1. Norma basalaris.

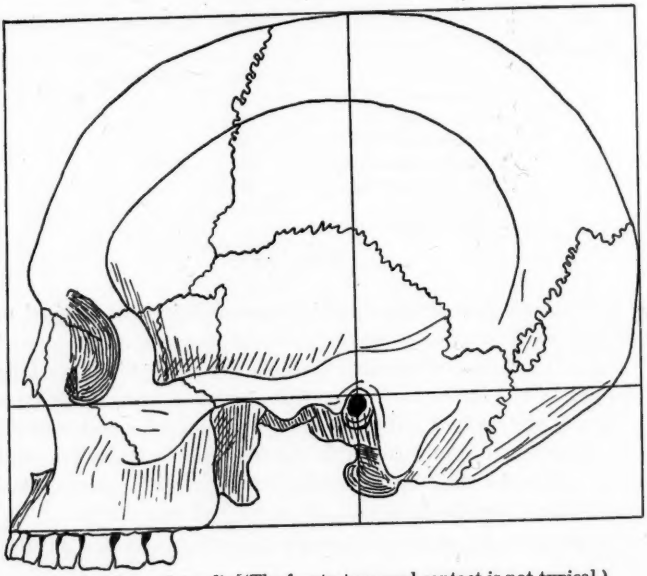

Fig. 2. Norma lateralis. (The fronto-temporal contact is not typical.)

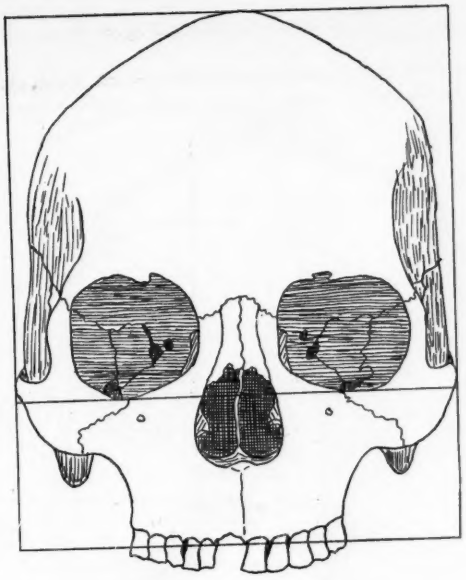

Fig. 3. Norma facialis

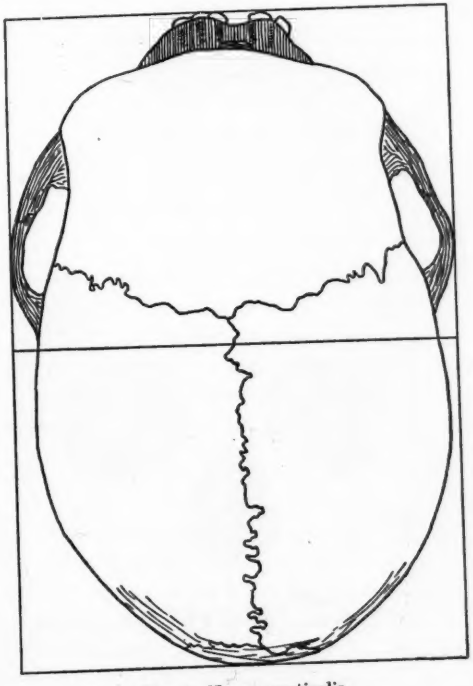

Fig. 4. Norma verticalis.

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Figs. 5–7. Female Australian from Queensland. R.C.S. 20. 3010.

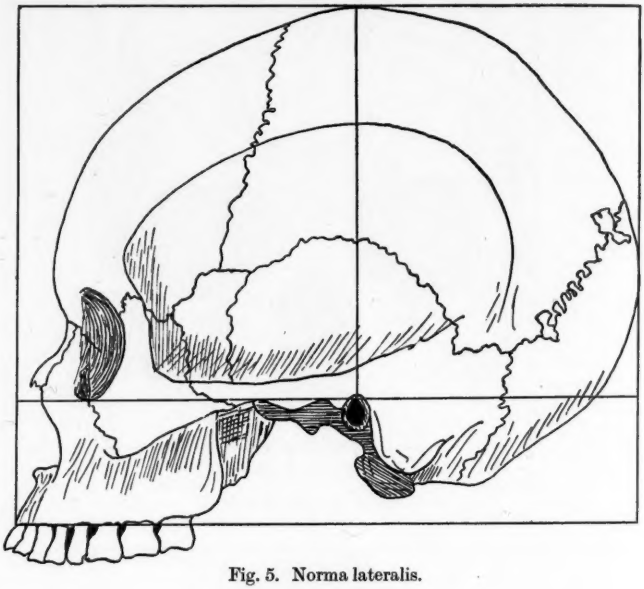

Fig. 5. Norma lateralis.

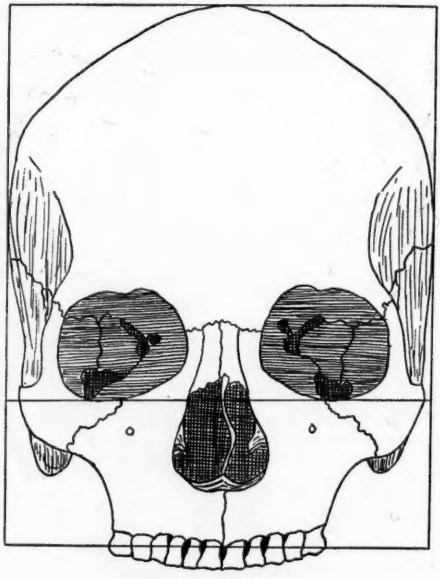

Fig. 6. Norma facialis.

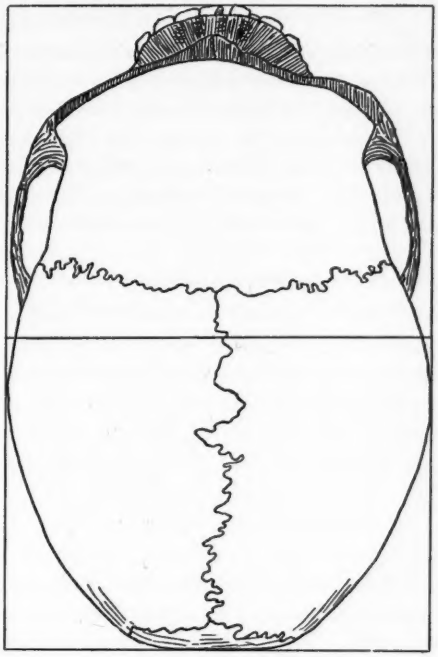

Fig. 7. Norma verticalis.

MORPHOLOGICAL FEATURES

(1) *Cranial form* (96 ♂, 60 ♀)

The male Australian cranium, as seen from norma verticalis, has the form of an elongate oval, with the anterior curve rounded, posterior tending to taper. In the majority of skulls the temporal fossa is not well filled, so that there may be a very evident post-orbital constriction, and the parietal boss is not excessively bulged. If, however, there is a tendency to parietal eminence it is not the parietal boss alone, but the entire parieto-temporal area that has expanded transversely. The occipital area is well developed, seen from norma lateralis, rising obliquely up and back from the foramen magnum to the inion, then vertically to lambda. The posterior portion of the skull is characteristically prominent as a pronounced occipital bulge. The female cranium, seen from norma verticalis, has the form of a pentagonal ovoid, for here the parietal bosses are well developed to present a marked lateral inflation. This, together with the tapered curve posteriorly and rounded curve anteriorly, presents a typical picture. The temporal fossa is not well filled, but slightly more so than in the male; nor is the occipital "planing" so marked.

(2) *Cranial asymmetry* (96 ♂, 61 ♀)

The Australian cranium, judging by careful visual appreciation from norma verticalis, is symmetrical to rather a high degree. In males 54 per cent., in females 51 per cent., of the skulls were either symmetrical or so slightly asymmetrical as to defy definition by the unaided eye. Of the males 27 per cent. had normal asymmetry, i.e. left occipital prominence, while 39 per cent. of the females evidenced the same. Reversed asymmetry, i.e. right occipital prominence, was noted in 19 per cent. of the males and 10 per cent. of the females.

(3) *Sutures* (96 ♂, 61 ♀)

If we record the degrees of sutural complexity numerically, 1, 2, 3, 4, 5 for linear, very simple, simple, complicated, highly complicated, then the Australian suture formula may be expressed as either C1, S2, L2 or C2, S2, L2, for both males and females, although the females tend to present a slightly higher average. In the males 40 per cent. are C1, S2, L2; 43 per cent. C2, S2, L2: in the females 9 per cent. are C1, S2, L2; 72 per cent. C2, S2, L2; and 9 per cent. attain C3, S3, L3.

(4) *Ossa suturarum* (98 ♂, 60 ♀)

These are found in 42 per cent. of the male, and 37 per cent. of the female skulls. Lambdoid ossicles were by far the most frequent, especially in the second part of the lambdoid suture, and were found more frequently on the right side than on the left. Of the 41 male skulls possessing lambdoid ossicles 82 per cent. were bilateral; of the 22 female skulls 85 per cent. In both male and female skulls 23 per cent. possessed multiple ossicles bilaterally. In the males ossicles occurred at asterion in 19 per cent. of the skulls, and in the females 12 per cent., the occurrence being slightly greater in the left side in both sexes.

In the total male series, there were ossicles at lambda in 9 per cent. of the skulls, and in the females in but 3 per cent. There were no ossicles at bregma in either sex. There were three instances of an os inca in the males and one in the female, and one os triangulare in the males. In only one skull (male) were ossicles in the occipito-mastoid suture observed, and in this skull they were present bilaterally. There were no instances of a metopic suture in either the male or female skulls.

(5) *Type of pterion* (98 ♂, 56 ♀)

In the male skulls 69 per cent., and in the female skulls 55 per cent., had the normal full bilateral alisphenoid-parietal articulation (Pterion H). For the males the width of the alisphenoid-parietal contact was: right, 8·00 (65 skulls); left, 8·09 (64 skulls); females: right, 6·95 (40 skulls); left, 6·86 (36 skulls). In both males and females the contact was 5 mm. or less in 26 per cent. of the skulls noted.

There were, in the males, two skulls with fronto-temporal articulation on

the right, and four on the left. In the females two had such articulation on the right, two on the left, and two bilaterally.

Epipteric bones, either unilateral or bilateral, were present in the males in 26 per cent. of the skulls and in the females in 36 per cent. In the males 4 per cent. possessed bilateral and fairly symmetrical epipterics, while 12 per cent. were unilateral on the right side and 10 per cent. on the left. In the females 5 per cent. possessed bilaterally symmetrical epipterics, while 12 per cent. were unilateral on the right side and 18 per cent. on the left. It is thus obvious that with regard to the total series neither side has pre-eminence in the matter of the unilateral epipterics. It is, however, to be noted that in the six skulls where the epipteric has continued as a separate ossicle along the squamous the right side presents three instances, the left two, while in one skull the occurrence is bilateral.

(6) *Supra-orbital foramina, notches, and grooves* (96 ♂, 61 ♀)

Bilateral notches were present in 74 per cent. of the male skulls and 60 per cent. of the female skulls, while bilateral foramina were present in 5 per cent. and 8 per cent. respectively. The notch and foramen may be found in the following combinations: notch right, foramen left, in males 15 per cent., females 6 per cent.; notch left, foramen right, in males 10 per cent., females 15 per cent.

Accessory foramina (f. frontale) are not very frequent. In the male skulls they are found, unilaterally, 3 per cent. on the right, 2 per cent. on the left, and only 1 per cent. bilaterally. In the female skulls there is only one case of a unilateral (left) accessory foramen; and in the female skulls, especially, are to be found instances with neither notches, nor foramina, to the extent of *ca.* 6 per cent.

With the exception of but one or two ill-defined instances the Australian skull does not present grooves upon the frontal bone.

(7) *Anterior ethmoid canal* (79 ♂, 54 ♀)

In the male skulls the canal has its normal sutural outlet in 75 per cent. of the cases, and in the female skull in 83 per cent. There is a bilateral frontal exit in 21 per cent. of the male skulls and 9 per cent. of the female skulls. A unilateral frontal exit on the right side is found in 4 per cent. of the males and 2 per cent. of the females, while a corresponding unilateral exit on the left side is found only in females in 6 per cent. of the skulls. In no case did the canal find exit in the lamina perpendicularis of the ethmoid.

(8) *Suture of the inner wall of the orbit* (79 ♂, 54 ♀)

In 98 per cent. of the male skulls and 100 per cent. of the females the normal relations were found. In two male skulls the maxillary bone had pushed very far back, in one there was a very narrow lachrymo-ethmoid articulation, and in one there was a direct fronto-maxillary articulation.

(9) *The spheno-maxillary fissure* (84 ♂, 52 ♀)

In the male skulls 43 per cent. of the fissures were linear or narrow, and of these about half were expanded antero-laterally. In the females the fissures were linear or narrow in 63 per cent. of the cases, and again about half had the antero-lateral expansion. In the males 37 per cent., and in the females 29 per cent., of the fissures were of average width, such as one would note in a European skull, while for males and females, respectively, 20 per cent. and 9 per cent. were much wider, especially anteriorly, than is usually the case.

(10) *Form of orbit* (95 ♂, 61 ♀)

The form of the orbit, as viewed from norma facialis and classified by mere inspection, depends for its analysis upon two factors: the shape of the aperture and the inclination of its longitudinal axis with reference to the face. Roughly speaking these two factors are found in Australian skulls with a frequency as shown in the following:

Male		Female	
Axis	Shape of aperture	Axis	Shape of aperture
Oblique 86 %	82 % angular 18 % rounded	Oblique 46 %	86 % angular 14 % rounded
Horizontal 14 %	70 % angular 30 % rounded	Horizontal 54 %	82 % angular 18 % rounded

There seem to be two facts worthy of note here, viz. the apparent sex difference in the axial inclination, and the general angularity of the aperture. In the male skull the supra-orbital complex is very pronounced, extending across the median plane in many instances to present a prominence at glabella so that nasion is relatively depressed. This results in the "beetling over" of the brow. Laterally the supra-orbital seems to continue on to the zygomatic process of the frontal bone and to push the lateral margin of the orbit down, as it were, emphasising the perpendicularity of the lateral orbital margin. Seen from norma lateralis the margin of the orbit rises vertically up to the fronto-malar suture and then slopes abruptly antero-superiorly.

With respect to the general obliquity of the orbit I must record the impression that some of it, judging by mere appearance, is fictitious: (1) the infero-medial margin of the orbital aperture inclines upward markedly; (2) the infero-lateral margin is not well defined and slopes on to the malar; (3) the heavy orbital process of the frontal, with its downward thrust, seems to "push" the lateral aspect of the orbit before it.

As a rule the obliquity of the orbit tends to be bilateral, though the degree of this condition may vary from side to side. When this occurs the right side seems to be the more oblique in the majority of the cases.

(11) *The infra-orbital canal* (96 ♂, 60 ♀)

In 82 per cent. of the males and 83 per cent. of the females the canal was single. There was an accessory foramen on the right side only in 5 per cent. male and female; on the left side only in 7 per cent. male and 5 per cent. female; and bilateral in 6 per cent. male and 7 per cent. female. In only one male skull, however, and that on only the left side, was the foramen double in the pithecoid sense. In all other cases there was one large normal foramen, and a smaller, medially placed accessory foramen.

In three male skulls the normal infra-orbital foramen possessed, bilaterally, at its superior median margin a small suture which ran up to the inferior margin of the orbit and from thence either to terminate in the infra-orbital sulcus (two cases) or the lachrymal canal (one case). In three female skulls, bilaterally, a suture proceeded from the superior lateral aspect of the normally placed infra-orbital foramen to the maxillo-malar suture, and from there the latter sent an accessory suture to the infra-orbital sulcus, thus setting off a small island of bone in the floor of the orbit. Four female skulls exhibited the same condition, with the exception that on the left side the anomalous suture proceeded from a medially placed accessory suture.

(12) *Form of the jugal* (95 ♂, 59 ♀)

The jugal is generally slight, in contrast to the massiveness of the upper facial features and the large palatal region. In the males 69 per cent. were classified as slight, while 17 per cent. were moderately heavy, and 14 per cent. were massive. For the females the corresponding proportions were 61 per cent., 30 per cent., and 9 per cent. Seen from the front the inferior margin tends to be horizontal, but seen laterally the jugal slopes up and backward markedly, this sloping being found in practically all of the skulls (98 per cent. of the males, 97 per cent. of the females). In a considerable number of skulls, particularly males, the inferior margin of the maxilla is concave superiorly, so that the lower portion of the maxillo-malar suture (facial aspect) is situated on a downward projection lateral to the concavity.

In no skulls, either male or female, were subdivisions of the malar bone noted.

(13) *The nasal bones* (94 ♂, 56 ♀)

The nasal bones are typically narrow superiorly, the average for the males, at the point of greatest constriction, being *ca.* 8 mm. and for the females *ca.* 10 mm. According to this classification approximately 70 per cent. of both males and females fall within the narrow group. It must be noted that the nasal bones tend to the shape of an hour-glass, with a much smaller superior portion above the constriction and a larger portion inferiorly which flared considerably. As to inequality in size, right and left, the occurrence was so infrequent that it was not recorded. The length of the nasal bones is equivocal. I classified, for

the males, 51 per cent. as short and 49 per cent. as long, while for the females the figures were exactly reversed.

In only one skull, that of an aged female, was the nasal suture synostosed.

(14) *The narial aperture* (93 ♂, 61 ♀)

In both males and females the narial aperture may be classified as large pyriform in shape, and medium in breadth, with males slightly broader (male average 28–30 mm., female 24–26 mm.). In the males 83 per cent. were pyriform and 17 per cent. oval or rounded, and of the pyriform 80 per cent. were large and 20 per cent. small. In the females 89 per cent. were pyriform, and 11 per cent. oval or rounded, and of the pyriform 65 per cent. were large and 35 per cent. small. The narial margins are usually double and in 16 per cent. of the males and 3 per cent. of the females a fossa praenasalis is to be observed. As a rule, the inferior narial margin is not sharply delineated but slopes downward on to the alveolar portion of the maxilla. A more or less sharply defined margin was found in 18 per cent. of the males and 21 per cent. of the females.

Subnasal prognathism (so-called alveolar prognathism) is present in both males and females to quite a marked degree, though not so pronounced as in the African Negro, for there were no cases in which the incisors approached procumbency.

(15) *Nasal septum* (61 ♂, 39 ♀)

The inclination of the nasal septum can be best summed up as follows:

	Medial	To right	To left
	%	%	%
Male	34	40	26
Female	36	41	23

The data yield nothing of significance.

(16) *The foramen ovale* (97 ♂, 54 ♀)

The foramen ovale was normal in position, shape, and size in 59 per cent. of the males and 55 per cent. of the females. It was normal in position, but either elongate or very large in 31 per cent. of the males and 24 per cent. of the females, and very small in 10 per cent. of the males and 21 per cent. of the females. In these cases the condition was generally bilateral.

The posterior bar of the foramen was very thin or a mere spicule of bone in 5 per cent. of the males and 8 per cent. of the females, the conditions being bilateral in all cases. In several skulls the foramen was bilaterally incomplete medially, but widely separated from the foramen spinosum. In three male skulls it was confluent with the foramen spinosum, one case being unilateral on the right side, two being bilateral. In six female skulls there was a similar confluence, two unilateral left, two unilateral right, and two bilateral.

As a rule the irregularities in the foramen ovale were compensated for by the presence or variation of the foramen of Vesalius, but figures of exact correlation are not calculated.

(17) *The foramen of Vesalius* (94 ♂, 58 ♀)

The data here may be summed up as follows:

	Absent	Present bilaterally	Present right side only	Present left side only
	%	%	%	%
Male	84	7	4	5
Female	88	5	2	5

The foramen is absent to a rather high degree in both sexes. There is no appreciable sex difference or priority of right or left side.

(18) *The foramen spinosum* (88 ♂, 56 ♀)

The foramen spinosum was present as a complete bony canal in its normal position in the spina angularis in 64 per cent. of the males and 50 per cent. of the females. In 9 per cent. of the females it was absent on the right side and normally complete on the left, and in one male skull it was absent on the left, present on the right. In 19 per cent. of the males and 27 per cent. of the females, however, it was bilaterally incomplete on its medial aspect. In 7 per cent. of the males and 9 per cent. of the females it was incomplete unilaterally on the right side, and on the left side in 6 per cent. of the males and 4 per cent. of the females. In all of the skulls the foramen, whether a complete bony canal or not, was situated in its normal position in the spina angularis. There were several cases where the spina angularis was unusually prominent and slightly re-curved on itself, so that the foramen spinosum was doubly perforate.

(19) *The spina angularis sphenoidei* (94 ♂, 58 ♀)

In 83 per cent. of the males and 88 per cent. of the females the spina angularis was a prominent blunt spur, i.e. it was long, tapering, but not pointed. In 12 per cent. of the females and 7 per cent. of the males it was a small, rather sharply pointed spur, and in 8 per cent. of the males only it was merely a rounded eminence. In 2 per cent. of the male skulls it was of such length that, curved slightly laterally, it merged with the lower margin of a very large lateral pterygoid lamina. In one male skull an anomalous suture ran from the spheno-temporal suture on the left side to isolate the spina angularis as a distinct bone. The foramen spinosum was situated upon this suture in this instance. In one female skull the tip of the spina angularis was united with a pronounced bony spur thrown up by the temporal bone just anterior to the carotid foramen, forming a complete foramen. This was bilateral.

(20) *The laminae pterygoidei* (89 ♂, 58 ♀)

In all of the Australian skulls, both male and female, the lateral pterygoid lamina was markedly wider than the medial, and in addition was splayed outward to a notable degree. In 32 per cent. of the males and 21 per cent. of the females the lateral lamina was very wide (15–20 mm.), and in 12 per cent.

of the males and 9 per cent. of the females was of unusual width (20 mm. and over). As previously noted, there was a tendency for the tip of the lateral lamina to contact with the tip of the spina angularis, and when such a pterygospinous bar was complete it passed medial to the foramen ovale.

(21) *The jugular foramen* (100 ♂, 57 ♀)

	Equal	Right larger	Left larger
	%	%	%
Male	22	66	12
Female	50	40	10

The foregoing table summarises the observations on the jugular foramen. The noteworthy feature is the apparent sex difference in that there appears to be greater equality between the right and left sides in the female. Actually, the right side, where there is inequality, has marked pre-eminence, for in the males in 48 per cent. and in the females in 34 per cent. of such cases the right side is twice as large, or larger, than the left.

(22) *The tympanic* (97 ♂, 60 ♀)

In 82 per cent. of the males and 93 per cent. of the females the tympanic forming the floor of the mouth of the external auditory meatus was of its normal thickness. The remainder of the cases were noted as being quite thin at the lateral margin. In one male skull, on the right side, the entire anteroinferior portion of the tympanic was absent, due to congenital malformation.

(23) *The foramen of Huschke* (90 ♂, 56 ♀)

In 94 per cent. of the males and 93 per cent. of the females the foramen was absent. In the males the foramen was present once on the left side only, twice on the right side only, and once bilaterally. In the females it was present once on the left side only and three times bilaterally.

(24) *The styloid processes* (82 ♂, 57 ♀)

The styloid processes were present in 84 per cent. of the males and 70 per cent. of the females, and absent in 16 per cent. and 30 per cent. in males and females respectively, so that the process is absent twice as much in females as in males. Where they occurred the processes were large, or very large, in 32 per cent. of the males and 22 per cent. of the females; medium, or small, in 26 per cent. of the males and 33 per cent. of the females; and very small, or rudimentary, in 42 per cent. of the males and 45 per cent. of the females. It was noted, especially in the male skulls, that there was a tendency for the vagina processus styloidei to be so large as to completely ensheath the styloid process in its proximal two-thirds.

(25) *Posterior condyloid foramina* (90 ♂, 56 ♀)

The observations may be tabulated as follows:

	Present	Absent bilaterally	Absent left, present right	Absent right, present left
	%	%	%	%
Male	56	25	15	4
Female	61	25	5	9

It will be seen that there are no significant differences either with reference to sex or right- and left-sidedness. Where the foramina are present about 25 per cent. in both male and female are unusually small, and in the majority of these cases the surrounding bone is pitted with many small (vascular?) foramina. It was observed as a general rule that where the foramen was large the fossa was also, and *vice versa*.

THE PROBLEM OF THE DEFINITION OF "AUSTRALOID"

Whenever a skull is encountered which "looks like" an Australian skull, but which cannot be one by virtue of its provenience, either geographical or chronological, it is termed "Australoid," often explained by supposing there has been contact in time and space.

Quite apart, therefore, from the analysis of the Australian skull type, *per se*, we must consider the matter of the elusive and oft-labelled Australoid. One need but go over the literature to ascertain the omnipresence of such an ephemeral definition-defying racial hybrid. It becomes of moment, consequently, to discover the trait or traits upon which the statement, in any given instance, of "Australoid" is based.

As a matter of fact, our problem is one which centres about the term "looks like." We are concerned with the degree of resemblance: whether or not the skull to be compared is similar in one or more of a number of morphological criteria.

The Australian skull has often been termed the most primitive of modern cranial types, and it is this characteristic, I think, which is responsible for the reference of a primitive-looking skull to the Australian type. But, since definite affinity is most frequently doubtful or improbable, the term "Australoid" is used to denote a possible relationship, or at least to connote similarity in appearance.

The facial view of a mental-composite male Australian (which is really what an average or type amounts to) may be analysed in an attempt to set forth those features conducing to the definition of "primitive." Were I to set down, in order, the four features which struck me as outstanding, I should write: (1) size, and rectangularity of orbits and massiveness of brow; (2) width and relative slightness of middle face; (3) size of palatal arch and teeth; (4) narrowness of frontal portion of vault. Let us, therefore, consider these in some detail.

The mass impression of the orbital apertures is imparted by the term "cavernous." They seem very large for the face, and are pronouncedly angular with the horizontal (so-called, but generally slightly oblique) axis the longest. They are surmounted by massive, "frowning," brow ridges which continue across the median plane and laterally contribute to an unusual degree to the lateral margin of the orbit. The impression of relative smallness of size is further enhanced by a narrow inter-orbital breadth.

The middle face, comprising the narial aperture and malar arches, is quite wide, but tends to be rather slight in proportion. As a rule, the arches project laterally well beyond the cranial contour, but this does not suffice to give them prominence in the sense that a Mongoloid or Eskimoid "high cheek bone" would. They are imprisoned and dwarfed, as it were, between a large palate and a massive orbito-supra-orbital complex. The middle face further gives the impression of slightness due to the large pyriform narial aperture with its guttering margin and slender nasal bones.

The lower portion of the face seems to be "all teeth and arch," for the palate and teeth of the Australian are second only to the Tasmanian in actual and relative proportion. The size is accompanied by subnasal prognathism which thrusts the palate markedly forward. Again, therefore, we find an area which minimises the middle portion of the face and which stands out as a very definite morphological feature.

The massiveness of the upper face receives its crowning touch, literally, by the marked narrowness of the frontal portion of the vault, which seems to slope away from the face. This is due to the strongly developed linea temporalis which sweeps up and back, compressing the skull antero-laterally so that in approximately 40 per cent. of the skulls the minimum frontal diameter is found near the intersection of the linea temporalis with the coronal suture.

Apart from the face, the long, narrow, moderately high cranium, with pronounced occipital development (so that the post-porionic length is the greater), seems to be characteristic if not actually definitive. The mastoid is proportionately small, but all muscular impressions are very well marked, especially on the occipital bone.

So much for this summary. Were *all* of the traits enumerated to be found in the same skull, the inference of identity with, or kinship to, the Australian type would be justified. The real problem, however, arises when one or more are found associated with other features. The issue then becomes one of possible influence, either from a common precursor or through actual contact. But, if the several characters mentioned *are* primitive they may occur sporadically as an indication of a remote common heritage. Again, there is no reason, so far as is known, why any given essentially human morphological trait may not occur at random as a mere expression of the range of human variation. In conclusion, it must be stated that the use of the term "Australoid" is not warranted in describing "primitive" skulls partaking of the so-called primitiveness of the Australian skull. Indeed, the term is misleading if

used to indicate relationship where only a few of the morphological traits peculiar to the Australian skull type are found. It is the unique association of all of the traits which have been enumerated that really constitutes "Australoid" in the fullest sense of the word.

It remains for a more exact knowledge of race-crossing and, most important, *race evolution*, to differentiate clearly the Australian type and the forms from which it arose as well as those to which it may have given rise.

THE GROWTH IN LENGTH OF THE LONG BONES IN THE MADDER-FED PIG[1]

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INTRODUCTION

It has long been known that the bones of the limbs grow in length by additions to the ends of the diaphyses, that the increments are unequal at the two ends, and that the greater increment is constant in position for a given bone (Keith (12), Sharpey-Schafer (16)).

These facts have been established (1) experimentally, (2) by observation of the bones of madder-fed animals, and (3) lately by radiographic observations of the ends of human bones

Experimental. That the limb bones grow in length by additions to their ends was first demonstrated by Stephen Hales (8) in 1727. He pierced two small holes half an inch apart in the tibia of a growing chicken with a sharp-pointed iron. Two months later he found that the distance between the two marks was still the same. He concluded that the bone between the marks had not distended lengthwise over the period of two months, and thus experimentally threw doubt on the common belief in the interstitial growth of bone. Further, he noted that the bone as a whole had grown an inch in length and that the growth was mostly at the upper end of the bone. These fundamental experiments of Hales were repeated with minor modifications of technique and on different animals by Duhamel (4) (silver stylets, pigeon and dog), John Hunter (11) (lead shot, pig), Flourens (6) (silver balls, rabbit) and Ollier (15) (lead shot, rabbit). Gatewood and Mullen (7) have recently again confirmed the conclusions of these observers by placing shot at measured intervals in the bones of young rabbits.

Madder Feeding. The colouring of bone by madder, first described in England by Belchier (1) in 1736, was employed by Duhamel (5), John Hunter (11), Humphry (10) and Kölliker (13) to investigate the mode of growth of the long bones. By madder feeding Duhamel certainly demonstrated that the shaft grows in width by sub-periosteal deposit; but there appears to be some doubt whether he thus confirmed his conclusions from the silver stylet experiments concerning growth in length. It is generally presumed that John Hunter did confirm his conclusions from the shot experiments by observations on the long bones of his madder-fed pigs, thus noting that length is obtained by additions to the ends of the shaft, and that there is a greater increment at one end than the

[1] Based on part of a thesis (June, 1929) accepted by the University of Birmingham for the degree of M.D. ("Observations on the Growth of the Limb Bones in the Pig").

other; but these observations do not appear to be recorded by him. Humphry certainly noted these facts and explains "that extension of the shaft takes place most quickly and is most prolonged, at the end where the bone can best bear the weakening consequent upon the more rapid changes in the growing matrix; and that is usually the larger end."

Radiography. Harris (9) has recently demonstrated radiographically that transverse striations near the diaphysial ends of the long bones of a non-rachitic child could be accurately dated over a period of two years. These transverse striations are held by Harris to represent periods of relative cessation of growth, corresponding to illnesses. The fact that the intervals between them remain constant as the bones grow in length strikingly confirms the other evidence that growth in length takes place only at the ends of the diaphyses and provides a means of measuring the relative amounts of growth at the two ends of human long bones.

The situation and direction of the nutrient canal has also been used by Digby (3) to show the unequal amount of growth at the diaphysial extremities. Human long bones were sectioned longitudinally through the plane of the nutrient canal and the plane of the canal projected into the medullary cavity until a point was reached midway between the walls of the section. This point Digby supposed to be the site of primary ossification[1].

The present contribution to the subject is based on the measurement of growth increments, during given periods, to the ends of the diaphyses of the limb bones of madder-fed pigs. These measurements are sufficiently accurate to permit statements of the relative amounts and calculation of the relative rates of bone growth at the two ends of the diaphyses. A method of graphic representation has been employed to demonstrate these relative amounts and rates.

MATERIAL AND METHODS

I am indebted to Prof. Brash for placing at my disposal the limb bones of a dozen madder-fed pigs varying in age between 80 and 587 days. These pigs came from three separate litters, were of mixed breed (sow, middle-large white; boar, Berkshire), and had all been castrated or spayed according to sex. They had all been fed from weaning with barley meal and "sharps" to which madder had been added; and in the case of one of the litters the sow had also been madder-fed for a fortnight before she farrowed and during lactation.

[1] The ulna in the pig is an exception to the general rule that the shaft grows in thickness by sub-periosteal addition on all sides. Instead of deposit there is some absorption on the ventral surface of the shaft which is contiguous to the dorsal surface of the radius. There is deposit on the medullary side of the ventral wall of the shaft of the ulna, and thus a growth movement of the shaft as a whole in a backward direction away from the radius. It is clear that Digby's proposition that the point in the centre of the medullary cavity in the line of the prolonged nutrient canal indicates the site of primary ossification can only be true of bones whose shafts can be shown to increase uniformly in thickness in all directions (this point is referred to more fully in my thesis).

All the pigs grew well as evidenced by steadily increasing weights. Their ages and details of madder and non-madder periods are noted in the following table. The horizontal lines separate pigs of different litters. (Pigs Nos. 12, 9 and 8 belong to the same litter.)

Table I

Pig No.	Age days	Madder period days	Growth without madder days
14	80	72	8
15	91	77	14
16	108	84	24
17	126	105	21
12	140	61	28
1	169	68	29
2	197	97	28
3	225	125	28
4	279	153	54
6	362	207	84
9	475	271	126
8	587	394	116

The madder was withdrawn from the food for varying periods, increasing according to the age and consequent diminution in rapidity of growth, before the animals were slaughtered. They were thus treated by the "indirect madder method" (employed by Duhamel, John Hunter and Humphry) whereby the new bone of the non-madder periods shows up white against the background of the thoroughly maddered skeleton. A short discussion of the advantages and disadvantages of the "direct" and "indirect" madder methods will be found in the paper by Prof. Brash (2) on "The growth of the alveolar bone."

The skeletons were macerated in a weak solution of KOH (0·1 per cent.) at 50° C., a method which appears to emphasise the contrast between the "old red" and "new white" bone.

The epiphyses of the limb bones separated readily except in the case of the oldest animals in which the bony union of the distal humeral and proximal radial epiphyses was first seen in No. 6 (362 days). No additional epiphyses had united in No. 9 (475 days). In the oldest pig, No. 8 (587 days), in addition to the above two, the distal tibial epiphysis had also united. It has been possible to ascertain from bones of older pigs that at 647 days in addition to the foregoing, the proximal ulnar, femoral, and the distal fibular epiphyses have united. The remaining epiphyses, distal radial, ulnar, femoral, proximal humeral, tibial and fibular, have united in a pig aged 729 days.

Before sectioning the diaphyses in order to measure additions of new bone at the ends, observations were made on the surface distribution of new bone, on the position of "stationary" areas and areas showing active absorption. Full details of these observations were recorded in the original thesis, and an account given for each bone of the "modelling process" (first described by John Hunter for the neck of the femur and in greater detail for other bones by

Kölliker) by which bones retain their shape as they grow in length and thickness. The only point to be noted here is that the addition of new bone to the ends of the diaphyses is obvious at a glance, since the white ends are invariably separated from the white bone surrounding the middle of the shaft by areas of older red bone (varying in extent according to the length of the non-madder period) with or without evidences of absorption according to the contour of the surface. These areas of absorption may and frequently do extend from the older red over the new white bone almost to the edge of the expanded growing ends of the diaphyses.

THE GROWTH IN LENGTH OF THE DIAPHYSES

In order to obtain reasonably accurate measurements of the amount of new bone added to the ends of the diaphyses longitudinal sections were cut. The bones of the left side were used for this purpose, and before the sections were made the maximum length of each diaphysis was taken on the osteometric board. The maximum lengths of the diaphyses are recorded in Table II. The lengths of a few of the older bones were measured in section as one of their epiphyses had united. These measurements are indicated in italics.

Table II. *Measurements of length in cm.*

Pig No.	14	15	16	17	12	1	2	3	4	6	9	8
Age in days	80	91	108	126	140	169	197	225	279	362	475	587
Humerus	9·5	9·6	10·0	10·7	10·8	10·5	11·4	12·2	11·9	*12·0*	*12·5*	*15·0*
Radius	7·1	7·0	7·6	7·7	8·4	7·7	8·8	9·3	9·2	*10·3*	*10·0*	*12·5*
Ulna	10·0	9·9	10·6	11·0	11·9	11·1	12·6	13·4	13·1	14·6	14·3	17·9
Femur	11·5	11·5	12·2	13·2	13·6	12·9	13·8	15·8	15·5	16·4	15·7	19·4
Tibia	10·6	10·2	11·1	11·5	12·0	11·6	13·1	13·9	13·5	14·7	14·4	*17·0*
Fibula	9·1	8·6	9·6	10·0	10·8	10·1	11·4	12·1	11·7	13·0	12·9	16·1

The sections of the diaphyses were made through long axes corresponding to their maximum lengths, and in order to obtain the best display of the new bone at each end, the plane of the section was approximately sagittal for the humerus, radius and ulna, and approximately coronal for the femur, tibia and fibula.

On sectioning long bones prepared by the indirect madder method a beautiful demonstration is obtained of the mode of growth in length by addition to the ends of the diaphyses (figs. 1–4).

In each of these figures (1–4) the areas of bone unstained by madder are represented white. Those at the ends and surrounding the shafts of the diaphyses represent new bone laid down during the second non-madder period (29 days). The white area of bone on the inside of the shaft was laid down during the pre-madder growth. Bone stained by madder is stippled in the case of cancellous and black in the case of compact bone.

At each end of the diaphysis the new white bone already noted on the surface stands out in contrast to the old red bone of which the greater part of the shaft is composed. The whole end of the bone is white, and this new white

Fig. 1.

Fig. 2.

Fig. 3.

Fig. 4.

Fig. 1. Sagittal section of diaphysis of right humerus of pig 169 days old (No. 1).
Fig. 2. Sagittal section of diaphysis of right radius of same pig as fig. 1.
Fig. 3. Coronal section of diaphysis of right femur of same pig as fig. 1.
Fig. 4. Coronal section of diaphysis of right tibia of same pig as fig. 1.
Scale nat.

cancellous bone is usually separated from the medullary cavity by a layer of red cancellous bone. The thickness of the new white bone and of the older red cancellous bone which is absorbed as the medullary cavity extends, varies according to the length of the non-madder period. The transition from old to new bone is sharp and allows of fairly accurate measurements of the thickness of the new bone and certainly of accurate comparisons of the amount laid down at the two ends. In every long bone the increments at the two ends are found to be unequal and the greater increment constant in position for a given bone.

It should be noted here also that the contiguous surfaces of the diaphyses and epiphyses present a marked contrast which is best observed in section; while the ends of the diaphyses are entirely composed of new white bone, the diaphysial surfaces of the epiphyses, provided that the bones have been previously thoroughly maddered, remain red at the end of even the longest non-madder period. It is evident on section that epiphyses grow in size by peripheral additions except on their diaphysial surfaces, and that the contribution made by the growth of the epiphyses to the total length of a bone depends entirely upon additions to their joint surfaces beneath the articular cartilage. Macewen's (14) comment on the term "epiphysial cartilage" may in this connection be noted and emphasised. "This cartilage," he says, "might more appropriately be called diaphysial, as its more active portion pertains to the diaphysis."

Fig. 1. Sagittal section of diaphysis of right humerus of pig 169 days old (No. 1). Fig. 2. Sagittal section of diaphysis of right radius of same pig as fig. 1. Fig. 3. Coronal section of diaphysis of right femur of same pig as fig. 1. Fig. 4. Coronal section of diaphysis of right tibia of same pig as fig. 1. Scale nat.

MEASUREMENTS OF NEW BONE AT THE DIAPHYSIAL ENDS

The growth increments at the ends of all the diaphyses, as represented by the layer of new white bone laid down during the respective non-madder periods, have been measured in the axes of maximum length, and are recorded in Table III. Measurements in italics are for part only of the non-madder period, since the respective epiphyses have united during this period.

Table III. *Diaphysial growth. Measurements in mm.*

Pig No.		14	15	16	17	12	1	2	3	4	6	9	8
Age in days ...		80	91	108	126	140	169	197	225	279	362	475	587
Age of new bone ...		8	14	24	21	28	29	28	28	54	84	126	116
Humerus:	Proximal	3·0	2·8	3·4	3·5	4·4	4·2	3·0	2·3	3·5	4·2	6·0	5·0
	Distal	1·4	1·4	1·4	1·5	1·7	1·3	1·5	1·0	1·2	*0·5*	*0·5*	Nil
Radius:	Proximal	1·4	1·0	1·4	1·2	1·8	1·3	1·0	0·7	1·2	*0·5*	*0·5*	Nil
	Distal	2·8	2·2	2·6	2·8	3·2	2·8	2·3	2·0	3·7	4·0	8·0	5·2
Ulna:	Proximal	1·5	1·1	1·5	1·4	2·0	1·5	1·2	0·9	1·4	1·2	3·0	2·7
	Distal	3·0	2·3	2·5	3·0	3·3	3·0	2·8	2·2	3·2	3·8	7·8	5·0
Femur:	Proximal	1·8	1·7	2·5	2·5	4·8	3·0	1·3	1·5	2·5	3·0	4·0	3·0
	Distal	3·2	3·2	4·5	4·2	6·8	5·0	3·0	3·0	4·5	5·0	6·0	4·5
Tibia:	Proximal	3·8	3·2	3·3	4·0	6·4	3·5	3·5	3·4	4·5	5·0	7·8	5·5
	Distal	1·8	1·5	2·0	1·6	3·5	2·3	1·6	1·2	1·3	1·2	2·4	*1·5*
Fibula:	Proximal	3·5	3·0	3·2	3·7	6·2	3·2	3·3	3·0	4·1	4·6	7·6	5·0
	Distal	1·8	1·5	2·0	1·8	3·1	2·0	1·4	1·2	1·4	1·5	3·0	2·0

RATES OF GROWTH

Since the non-madder growth periods of the individual bones vary, having been increased with the age of the animal in order to obtain about the same amounts of new bone as the general rate of growth diminished, the growth increments cannot be directly compared. The table of measurements of new bone (Table III) shows the increments during periods varying from 8 to 126 days. In order to compare rates of growth in young and old bones the amount of new bone laid down at the proximal and distal diaphysial ends has been calculated per week (Table IV). Figures in italics are calculated in the same manner as the remaining ones, but from measurements of new bone over an unknown and shorter growth period than in the previous table, since growth must have ceased with the union of epiphyses in the situations indicated; consequently the rates shown are comparatively small.

Table IV. *Rates of diaphysial growth per week. Measurements in mm.*

Pig No.		14	15	16	17	12	1	2	3	4	6	9	8
Humerus:	Proximal	2·63	1·4	1·0	1·16	1·1	1·05	0·75	0·58	0·44	0·35	0·33	0·30
	Distal	1·22	0·7	0·4	0·5	0·42	0·32	0·38	0·25	0·15	*0·04*	*0·02*	Nil
Radius:	Proximal	1·22	0·5	0·4	0·4	0·45	0·32	0·25	0·18	0·15	*0·04*	*0·02*	Nil
	Distal	2·44	1·1	0·74	0·7	0·80	0·7	0·58	0·5	0·47	0·33	0·44	0·31
Ulna:	Proximal	1·31	0·55	0·43	0·46	0·5	0·37	0·3	0·22	0·17	0·1	0·16	0·16
	Distal	2·62	1·15	0·71	1·0	0·80	0·7	0·7	0·55	0·4	0·31	0·43	0·30
Femur:	Proximal	1·57	0·85	0·71	0·8	1·2	0·75	0·32	0·37	0·31	0·25	0·22	0·18
	Distal	2·80	1·6	1·3	1·4	1·7	1·25	0·75	0·75	0·55	0·41	0·33	0·27
Tibia:	Proximal	3·33	1·6	0·94	1·3	1·6	0·87	0·87	0·85	0·56	0·41	0·43	0·31
	Distal	1·57	0·75	0·57	0·5	0·87	0·58	0·4	0·3	0·16	0·1	0·13	*0·09*
Fibula:	Proximal	3·07	1·5	0·91	1·2	1·5	0·8	0·82	0·75	0·51	0·38	0·42	0·28
	Distal	1·57	0·75	0·57	0·9	0·77	0·50	0·35	0·3	0·17	0·12	0·16	0·11

From this table it is clear that there is a gradual diminution in the rate of growth in every bone as one passes from the younger to the older bones. In the youngest bones (80 days) the ends with the greatest increments have an average growth of 2·82 mm. per week, while the ends with the lesser increments have an average growth of 1·41 mm. per week. Therefore the ends with the greatest increments are making approximately twice the growth of the ends with the lesser increments at this age. At nearly a year old (362 days) the average growth of the ends with the greater increments is 0·37 mm. per week, while that of the ends with the lesser increments is 0·11 mm. per week, the ends with the greater increments making approximately three times the growth of the ends with the lesser increments.

About a year old the distal epiphysis of the humerus and the proximal epiphysis of the radius begin to unite, so that the increment shown for the diaphysial ends adjacent to these epiphyses in No. 9 (475 days) was laid down early in the non-madder period (126 days) and not throughout this period as in the younger bones. In No. 8 (587 days) union of the above-mentioned epiphyses took place before the non-madder period (116 days), and no new

bone is laid down at the diaphysial ends adjacent to these united epiphyses. The distal epiphysis of the tibia had united in No. 8 (587 days), so that the increment at this end of the diaphysis is that for the early part of the non-madder period (116 days).

As the epiphysial cartilage begins to disappear and the epiphysis unites with the diaphysis, growth in length at that end of the bone must cease, except in so far as the articular surface of the epiphysis itself may continue to grow.

It is also quite obvious from these tables that the greater growth in length at one end of a long bone is due not so much to the fact that the epiphysial centre of ossification appears earlier at one end and remains longer ununited there, but to the greater rate of diaphysial growth throughout the growth period, as originally pointed out by Humphry.

The rates of diaphysial growth of individual bones now being known between 80 and 587 days, it is possible, taking the length of the youngest bone as a starting-point, to calculate the growth increments that might be expected to be added to it at the stage of each successive older bone. The differences in age of the successive older bones do not always correspond to the non-madder growth periods, so that it is necessary to calculate from the rates of growth the amount of growth for these periods of differences in age. The results of these calculations are set out in Table V. Figures in italics, being calculated from those of the previous table which are for a shorter growth period than stated, are comparatively small.

Table V. *Expected growth increments of diaphyses. Measurements in mm.*

Pig No.		14	15	16	17	12	1	2	3	4	6	9	8
Age in days ...		80	91	108	126	140	169	197	225	279	362	475	587
Difference in age ...		—	11	17	18	14	29	28	28	54	83	113	112
Humerus:	Proximal	—	2·19	2·42	2·98	2·2	4·20	3·00	2·32	3·38	4·20	5·28	4·8
	Distal	—	1·09	0·97	1·28	0·84	1·28	1·52	1·00	1·15	*0·48*	*0·32*	Nil
Radius:	Proximal	—	0·78	0·97	1·02	0·9	1·28	1·00	0·72	1·15	*0·48*	*0·32*	Nil
	Distal	—	1·73	1·8	1·8	1·6	2·8	2·32	2·0	3·61	3·96	7·04	4·96
Ulna:	Proximal	—	0·86	1·04	1·18	1·0	1·48	1·2	0·88	1·30	1·2	2·56	2·56
	Distal	—	1·8	1·72	2·57	1·6	2·8	2·8	2·20	3·08	3·72	6·88	4·8
Femur:	Proximal	—	1·33	1·71	2·05	2·4	3·00	1·28	1·48	2·38	3·00	3·52	2·88
	Distal	—	2·66	3·15	3·59	3·4	5·00	3·00	3·00	4·23	4·92	5·28	4·32
Tibia:	Proximal	—	2·51	2·28	3·34	3·2	3·48	3·48	3·40	4·31	4·92	6·88	4·96
	Distal	—	1·18	1·39	1·29	1·74	2·32	1·6	1·2	1·23	1·2	2·08	*1·44*
Fibula:	Proximal	—	2·4	2·21	3·08	3·0	3·2	3·28	3·00	3·92	4·56	6·72	4·48
	Distal	—	1·18	1·39	2·31	1·54	2·0	1·40	1·2	1·31	1·44	2·56	1·76

The data provided by this table have been used to illustrate the relative rates and amounts of growth at the two ends of the humeral, radial, femoral and tibial diaphyses. The expected length of the diaphysis at each stage has been contrasted with the length of the actual specimen (figs. 5 and 6).

The horizontal base line represents 80 to 600 days on a scale of one day per 0·33 mm. The vertical scale represents length (scale $\times \frac{1}{3}$). The stippled areas represent the amount of expected increment at each end of the youngest

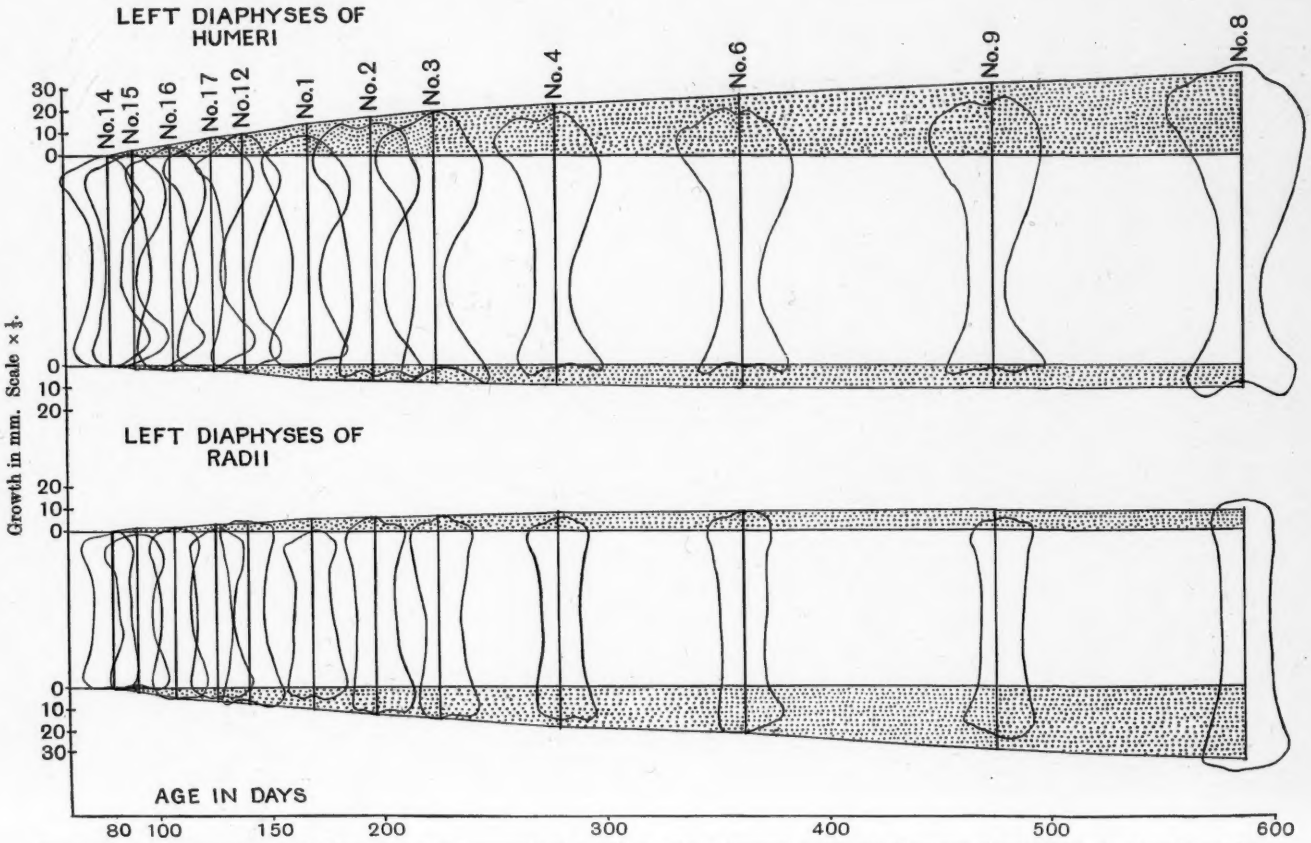

Fig. 5. Graphic representation of relative rates and amounts of growth at ends of humeral and radial diaphyses of madder-fed pig as explained in text.

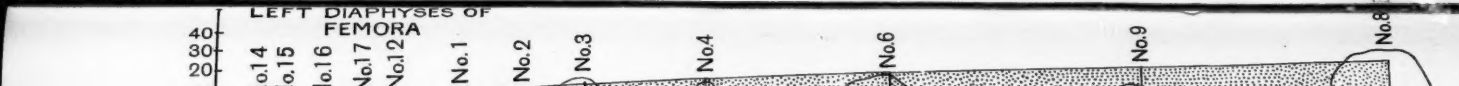

Fig. 5. Graphic representation of relative rates and amounts of growth at ends of humeral and radial diaphyses of madder-fed pig as explained in text.

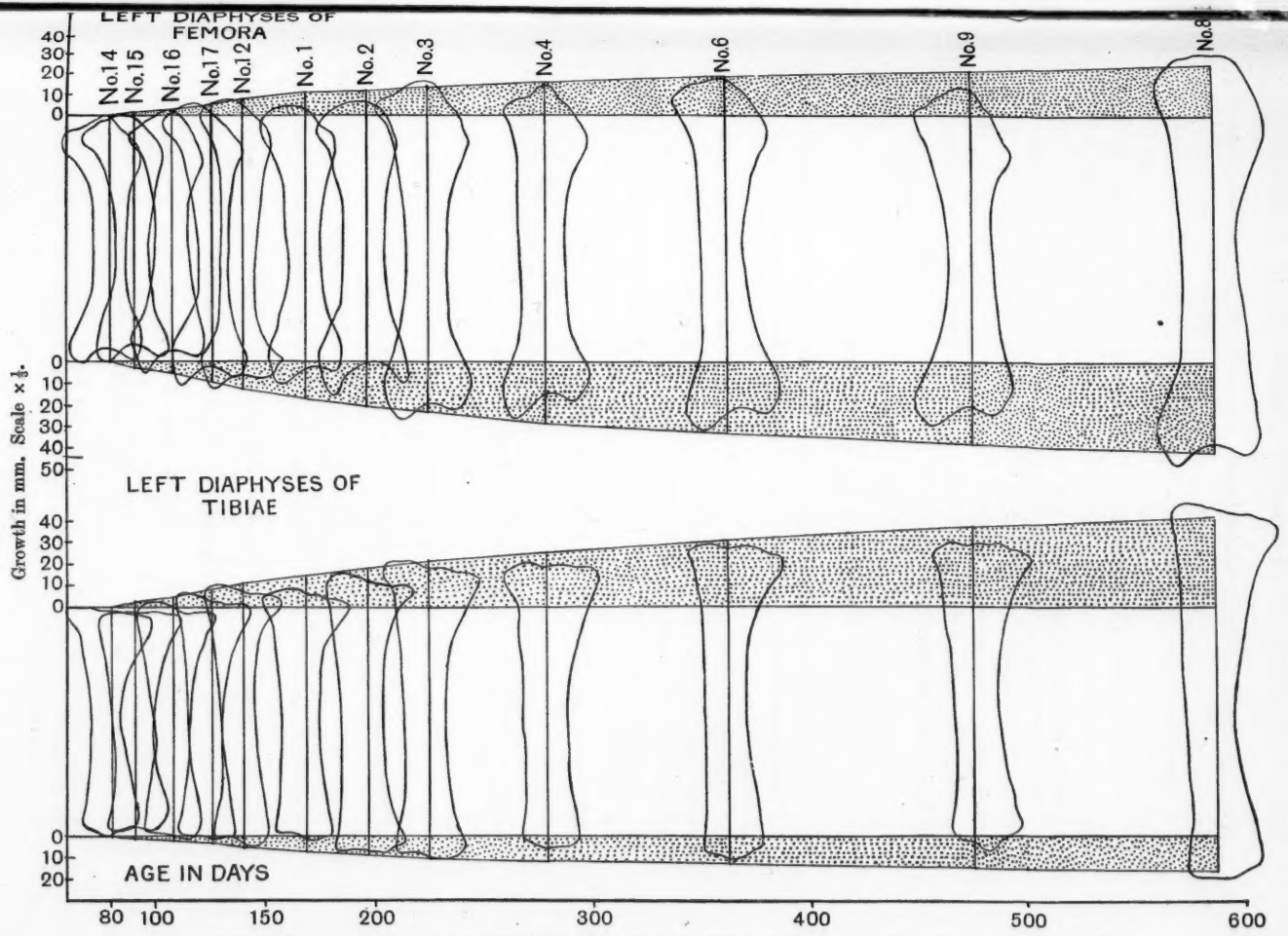

Fig. 6. Relative rates and amounts of growth at ends of femoral and tibial diaphyses of madder-fed pig. Scale as in fig. 5.

diaphysis and at the ages of the older bones a vertical line is drawn to represent the expected length which the youngest diaphysis might have reached. Over the expected length has been drawn the outline of the individual bone for comparison.

On this basis the diaphyses of the long bones of various ages may be superimposed in proportion to their growth in length to demonstrate the relative amounts and rates of growth at the two ends.

The fact that some of the diaphyses are shorter while others are longer than the expected length may be accounted for by the circumstance that we are dealing with the bones of individual pigs with mixed inheritance, though indeed it is notorious that individual pigs of pure breed also vary considerably in their rates of growth.

SUMMARY AND CONCLUSIONS

The amounts and quantitative ratios of new bone added to the two ends of the limb bones are demonstrated for the bones of madder-fed pigs over given periods.

The rate of growth diminishes with age, the diminution being more rapid at the end which has the lesser increment (the proportion of growth being 2 : 1 at 80 days as compared with 3 : 1 at 362 days).

From measurements of growth increments in madder-fed pigs it is possible to superimpose a series of long bones of increasing ages to show the relative amounts of growth at the ends of their long axes.

In conclusion I would like to express my thanks to Prof. Brash for his advice and help in the preparation of this paper.

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ANATOMICAL NOTES

FUSION OF CERVICAL VERTEBRAE

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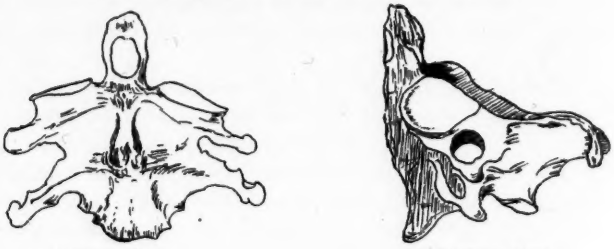
In the collection of bones in the Anatomy Museum of the Medical College, Calcutta, there are eight specimens of fusion of cervical vertebrae. These fusions are non-pathological, as there is an absence of any inflammatory thickening or other evidence of disease in the bones. These fused vertebrae are not traceable to the spinal columns of which they were parts, and hence they offer no clue to the condition of the vertebrae in other regions of the same axial column. There are five specimens of fusion of the 2nd and 3rd cervical vertebrae. There is one specimen each of fusion of the 4th cervical with the 5th, of the 6th cervical with the 7th and of the 7th cervical with the 1st thoracic vertebra. A detailed description of the specimens is given below.

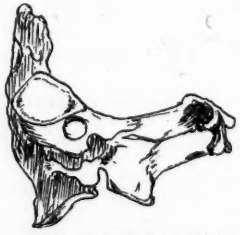
Fusion of the 2nd and the 3rd cervical vertebrae



Front view. Left lateral view.

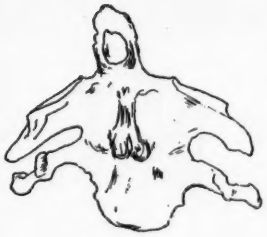
Specimen No. 1.

Specimen No. 1. There is complete fusion of the under surface of the body of the 2nd cervical vertebra with the upper surface of that of the 3rd. The laminae, the spinous processes and the adjacent articular processes are completely fused and only faint grooves indicating the lines of fusion are seen. The fusion of the spinous processes is so complete that no trace of the line of fusion is visible. The transverse processes, however, have not fused and are quite separate on both sides.



Specimen No. 2. Left lateral view.

Specimen No. 2. The fusion of the parts is the same as in specimen No. 1, and if anything more complete except in the case of the spinous processes where faint grooves are visible indicating the line of fusion.

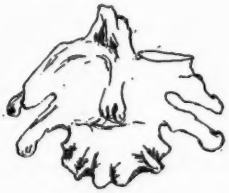


Front view.

Left lateral view.

Specimen No. 3.

Specimen No. 3. The odontoid process is slightly deflected to the right. The fusion of the parts is like that of the specimen No. 2. The spinous process of the 2nd cervical is not bifid and the gap between the adjacent transverse processes on the left side is greater than that on the right side owing to the greater depth of the body and the articular pillar of the left half of the 2nd cervical vertebra.



Front view.

Left postero-lateral view.

Specimen No. 4.

Specimen No. 4. The odontoid process is stunted and conical. The anterior surface of the body of the 3rd cervical vertebra is much prolonged inferiorly like that of a normal 2nd cervical vertebra. The fusion of the parts is like that of the specimen No. 3. The spinous process of the 2nd cervical is also not bifid. The superior articular processes of the 2nd cervical vertebra have flat surfaces looking upwards.

Front view.

Left lateral view.

Right lateral view.

Specimen No. 5.

Specimen No. 5. The fusion of the bodies of the two vertebrae is incomplete in the right three-quarters of the segment. The fusion of the right laminae is also incomplete. The left laminae are completely fused, a groove indicating the line of fusion. There is no fusion of the spinous and transverse processes. The right foramen transversarium is incomplete in the 2nd cervical vertebra.

Fusion of the 4th and 5th cervical vertebrae

Front view. Left lateral view.

Specimen No. 6.

Specimen No. 6. In this specimen the fusion of the bodies anteriorly is incomplete, a cleft on this aspect being visible. The anterior surface of the body of the lower vertebra is much prolonged inferiorly. The adjacent articular processes are fused but the laminae, transverse and spinous processes are not fused.

Fusion of the 6th and 7th cervical vertebrae

Front view. Right postero-lateral view. Left lateral view.

Specimen No. 7.

Specimen No. 7. The fusion of the bodies is incomplete in front where a cleft is visible. The adjacent articular and spinous processes, and the laminae of the left side are fused. But on the right side the fusion between the laminae and between the articular processes is incomplete. The laminae and the corresponding halves of the spinous processes of the two sides have not fused in the middle line. Moreover, the right half of the spinous process of the 7th cervical vertebra is on a lower level than its counterpart.

Fusion of the 7th cervical and 1st thoracic vertebrae

Top view. Right lateral view.

Specimen No. 8.

Specimen No. 8. The fusion of the parts is exactly like that seen in specimen No. 7. The costal process of the 7th cervical vertebra on the left side is not con-

nected laterally with the transverse process, and hence there is no foramen transversarium on this side. There are two such foramina on the right side of the same vertebra.

Commentary

Many instances of fusion of the occipital bone with the atlas (1), (3), (4) and of the atlas with the axis (2) have been reported, though they are not very common. Fusion of the axis and the 3rd cervical vertebra (4) is still rarer, although five specimens of such fusion are reported in this paper. The tendency to fusion of the segments is greater towards the cranial and caudal ends of the vertebral column. The occipital bone is formed by the fusion of at least three such vertebrae, the body of the atlas is normally fused with that of the axis and the tendency to fusion persists in the succeeding vertebrae, and it is possible that the tendency diminishes as we proceed caudalwards towards the lumbar region. Instances of non-pathological fusion of the vertebral elements towards the lower cervical region and in the thoracic and upper lumbar regions are very rare. It is difficult to infer from the specimens at which stage of development fusion actually occurred and whether these are instances of incomplete cleavage of the segments. It is noteworthy that the fused segments are associated with other developmental anomalies such as stunted growth and deflection to one side of the odontoid process (Specimens 3, 4), non-union of the two halves of the vertebral arch (Specimens 7, 8) and marked projection inferiorly of the anterior surface of the body of the 3rd cervical vertebra (Specimen 4).

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A CASE OF TERATOLOGICAL DUPLICATION IN THE SPARROW, *PASSER DOMESTICUS* L.

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On 20 June, 1931, a three-legged sparrow was sent to this laboratory as an object of interest by Mr Hugh Godsal of Twyford, Berkshire, who found it dead outside his house. A superficial examination showed that the bird was fully fledged and apparently about one month old; that the third leg possessed seven toes and was probably two legs fused together (confirmed later by dissection); and that there were two cloacal openings, one on each side of the fused extra legs, but the one on the right side was slightly dorsal and anterior to that on the left, i.e. the two openings were not symmetrical with regard to the general body axis of the animal. The tail had ten rectrices, five on each side of the middle line. The uropygial gland was normal.

Dissection of the middle leg confirmed the view that it was the result of the fusion of two limbs. The femora were completely fused and appeared as a single bone. The tibiae also were completely fused, but the two fibulae appeared as delicate splint bones one on each side of the fused tibiae. The tarso-metatarsi were incompletely fused. There were seven digits in two quite distinct groups of four and three respectively. One digit of the smaller group lacked a claw. The larger group slightly overlapped the smaller owing to the torsion of the fused legs. This torsion appeared in the distal part of the fused tibiae and extended to the extremity of the limb, being most in evidence in the case of the tarso-metatarsi and the digits. The result of the torsion was to give the right metatarsus a half turn over to the left, bringing the plantar surface of the feet into view as the bird lay on its back. The tibio-femoral joint was immovable, the tibiae and femora being inclined to one another at an angle of about 85°. The fused femora were short and the head was directed dorsalwards. To the head was attached a fragment of pelvis, the identification of which was uncertain. The comparative lengths of the parts of the middle legs and those of a normal leg were roughly as follows:

Normal tarso-metatarsus	2·0 cm.,	abnormal	1·6 cm.
„ tibia	2·8 cm.,	„	2·4 cm.
„ femur	1·8 cm.,	„	1·2 cm.

I was unable to find any connection between the extra legs and the normal pelvis.

On opening the body there were no signs of starvation, the rectum being very full and the fat body well developed. The stomach and anterior viscera were normal, but the posterior end of the intestine opened into a greatly dilated and pear-shaped chamber, which occupied a great part of the body cavity. The openings to the exterior occurred at the posterior angles of this dilated portion. It will be remembered that the cloaca of a normal bird is divided into three chambers. The anterior chamber or coprodaeum drains the rectum. It leads into the middle chamber or urodaeum which receives the urinary and genital ducts. The urodaeum leads into the posterior chamber or vestibule which communicates with the exterior. The dorsal wall of the vestibule bears the aperture of the bursa Fabricii. In this specimen there was found on each side a straight duct, communicating with the kidney of its own side, quite well developed, and clearly an ureter. Associated with each ureter laterally there was a second duct, poorly developed and having a swelling on it distally. The latter ducts would appear to be the vasa deferentia, although no testes were found. The

two ureters and the two vasa deferentia opened into the dilated region mentioned above, and since this chamber also receives the rectum it represents the two anterior chambers of the cloaca, the coprodaeum and the urodaeum, enormously dilated and not differentiated from one another, but with the normal number of ureters and vasa deferentia, viz. one pair of each, entering the urodaeum. In other words, the coprodaeum and urodaeum were not duplicated. On the other hand, the posterior chamber or vestibule was duplicated, there being two distinct and widely separated chambers, each opening to the exterior, and each clearly differentiated from the single, dilated urodaeum and coprodaeum. There was no bursa Fabricii associated with either vestibule.

The above abnormality appears to be a case of pygomelian duplicity. M. Fernand Lataste has described a somewhat similar case in the *Procès Verbaux of the Linnean Society of Bordeaux*, 1923, p. 146. In his specimen, a chicken, the two extra legs were separate. There were two cloacal openings, but whether or not the whole cloacal region showed a condition similar to that here described was not stated. M. Lataste also mentioned a duck having four separate legs and two cloacal openings, but again no details of the internal anatomy were given, the specimen not being available for dissection.

The specimen here described is now No. 2158 in the Zoology Museum of the University of Reading.

DEFECTIVE DEVELOPMENT OF THE SEPTUM PELLUCIDUM

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DURING the course of the dissections of the brain by the senior second-year students in the sixth terminal trimester of their Anatomy course corresponding to the winter session of this year, our attention was drawn by a batch of students to the abnormality described hereunder.

After exposing the corpus callosum from above and dividing it transversely at about its middle it was noticed that the usual septum intervening between the corpus callosum and the fornix (*Fo.*) was absent. There was, however, at the forepart of

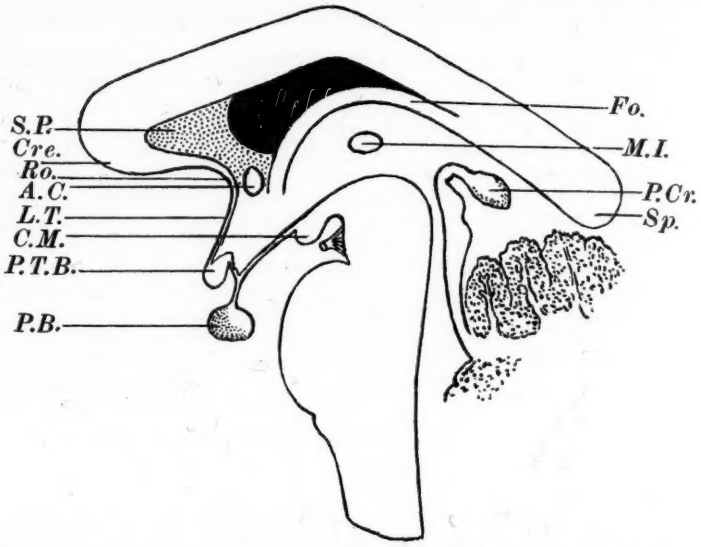

Fig. 1. Diagrammatic representation of the defective development of the septum pellucidum.

the interval the rudiments of a partition (*S.P.*) showing a concave posterior free margin. A section through the attenuated partition revealed the absence of any cavity in its interior, as it comprised a solid core of white matter surrounded by a thin layer of grey matter. This structure was adherent to the subjacent fornix. The normal septum described under the name of the septum pellucidum was found to be defective and confined to the forepart of the interval between the two lateral ventricles (see fig. 1).

This partition was about $\frac{1}{2}$ in. antero-posteriorly and $\frac{3}{8}$ in. from above downwards, having a trapezoid outline with its broader upper convex margin attached to the under surface of genu (*Cre.*) of the corpus callosum, its anterior concave

margin to the rostrum (*Ro.*) becoming continuous inferiorly with the lamina rostralis, below and behind to the anterior pillar of the fornix. The posterior margin, however, was blunt, crescentic and free. On making a sagittal section of the cerebrum the anterior commissure (*A.C.*) could be made out in its usual position. The condition was not pathological, as evidenced by the appearance of the parts.

The principal features of interest are:

1. The septum, though present, is defective.
2. It is solid and unilaminar.
3. The absence of the cavity of the septum pellucidum.
4. The free communication between the two lateral ventricles.
5. The foramina of Munro are smaller than normal.
6. The other structures constituting the Rhinencephalon are normally developed.

We have ventured to submit this article for publication as the abnormality described above is a rare one and as there is hardly any reference to it in the available works of reference here.

REVIEWS

A description of the planes of fascia of the human body. By B. B. GALLAUDET. (New York: Columbia University Press; London: Oxford University Press.) 1931. Price 14*s.* net.

The author states that the fascial planes in the abdomen, pelvis and perineum are very inadequately described in standard English and American text-books, and it is for this reason that he has carefully studied by actual dissection thirty-four adult human bodies, with the result that he has been able to write a short monograph on the subject.

On reading through the fifty-nine pages of which the book is made up, there does not appear to be anything in it which is new to the practical anatomist, and it is very irritating to constantly find such abbreviations as "int. obl." and "rectus abd." throughout the book.

The price of the book is prohibitive; it would be more likely to be purchased if it were published at 6*s.* net.

Das Arteriensystem der Japaner. By BUNTARO ADACHI (Professor der Anatomie an der Kaiserlichen Universität zu Kyoto). Kyoto. 1928.

In zwei Bänden. Mit 539 Abbildungen im Text und auf vier farbigen Tafeln sowie mit etwa 700 Tabellen.

Band I. Arteria pulmonalis, Aorta → Arcus volaris profundus. (SS. 440.)

Band II. Aorta thoracalis → Arcus plantaris profundus. (SS. 353.)

A significant phenomenon in the sciences to-day is the resort to the statistical method not only by those branches such as physics which have until recently been regarded as "exact" and therefore outside the field of the probability concept, but also by those branches at the other extreme which are sometimes called "descriptive sciences." The use of statistical methodology in anthropometry, craniometry, osteology and the newer branches of anthropology is well established, but its application to the study of internal anatomy marks a further and welcome advance. The monumental work on the arterial system of the Japanese by Prof. Adachi may well be regarded as the first serious attempt to study racial variation in regard to internal anatomy by such methods.

The keynote of Prof. Adachi's work may be summed up in two sentences, "Die Anatomie des Menschen ist die Anatomie der Menschen-rassen," and "Die heutige Anatomie des Menschen ist eigentlich nicht die Anatomie des Menschen im allgemeinen, sondern nur die Anatomie der Europäer." He sets out in these two large and beautifully produced volumes to remedy this state of affairs by comparing the arterial system of the Japanese, as studied from several hundred cadavers at the Institutes of Anatomy at Okayama and Kyoto, with that described by European and American anatomists, bringing into play for the purpose the usual statistical tests for the significance or otherwise of the differences noted.

Hitherto the comparative anatomy of different races has been almost confined to external measurements and studies of the skeletal and muscular systems, and on the whole the results have been disappointing as providing any sure method of unravelling the intricacies of Man's genetic history. The study of haemolytic reactions has recently provided new methods of classifying mankind into blood groups which it was

hoped would throw more light on this problem, but the limitations of these methods of analysis also are already becoming evident. The detailed study of the internal organs, and especially of the arterial and peripheral nervous systems might conceivably provide us with unsuspected and hidden keys, but so great is the task of charting these systems in a sufficient number of individuals of different racial groups that it is not surprising that anatomists have not hitherto taken up the task with enthusiasm. Prof. Adachi has courageously set the example for the Japanese, and a careful study of his work will enable other anatomists to decide whether the results of this great labour are sufficiently suggestive to encourage others to follow in his footsteps.

It is not possible in a short review to detail all the respects in which the arterial system of the Japanese is found to differ significantly from that of Europeans, but the most important are the less frequent origin of the superior laryngeal, ascending pharyngeal and ascending palatine arteries as direct branches from the external carotids, and of the obturator arteries from the external iliac arteries, the more frequent common origin of the subscapular with the posterior circumflex humeri artery and of the superior profunda brachii with the inferior profunda brachii artery, the more frequent origin of the nutrient tibial from the anterior tibial artery, the less frequent "high division" of the popliteal artery and the less frequent occurrence of the simple form of anterior communicating artery in the circle of Willis. The internal maxillary artery occupies a medial position in relation to the external pterygoid muscle ten times as often in Europeans as in Japanese, and there is a correlation of 0·53 between the right and left arteries in this respect. The level of the arch of the aorta in relation to the thoracic vertebrae is found to sink with advancing age, the correlation with age being of the order 0·66. The height of the bifurcation of the common carotids is found not to differ significantly on the two sides in the Japanese, though this has been stated, perhaps on insufficient evidence, to be the case in Europeans.

Little criticism is called for of the author's handling of his data or of the conclusions he has drawn therefrom. An error however was noticed on page 152 of Volume II, where the frequency of occurrence of the truncus profundo-circumflex perfectus in "Europeans" should be 439 in 827, or 54·8 per cent., compared with 63·2 per cent. in 367 Japanese, the difference being $8{\cdot}4 \pm 3{\cdot}1$ per cent. and therefore of doubtful significance.

The volumes are admirably produced and copiously interspersed with over 500 illustrations and 700 tables. Though disappointment may perhaps be occasioned by the outcome of this search for outstanding racial differences in the arterial system, this thorough piece of work will remain of permanent value not only as a source of reference in regard to the arterial system in general but as a model for scientific study of the internal anatomy of a racial group.

A theory of the formation of animals. By W. T. Hillier, M.R.C.S., L.R.C.P. (Bristol: John Wright and Sons, Ltd.) 1932. Pp. iv + 166, 98 figs. and 7 plates. Price 8*s.* 6*d.* net.

This is a fanciful book, and on that account is difficult to assess, without unintentionally doing an injustice to the author.

The basal idea underlying the author's hypotheses, is the dual constitution of every sexually produced animal. Upon this plain observable fact he builds a series of assumed or imaginary designs (comparable to theoretical designs in engineering construction) that he thinks govern the processes of development, and are of such a nature that throughout the sequence of events the individuality of each parent constantly asserts itself, resulting in an obscure duplication of parts.

The idea, at its simplest, is illustrated by the gastrula, which in the author's view

consists of two blastulae, one inside the other, one being an expression of the one parent and the other of the other.

In later chapters this idea of the dual constitution of the body is elaborated in a review of the development of Polygordius and of the adult structure of the Herring, and the author attempts to show how the general development of Polygordius and the cell lineages traced by Woltereck can be explained by the rotation of hypothetical bi-parental blastulae upon certain axes.

In this attempt the author shows great and praiseworthy ingenuity, but he will probably, as he himself expects, find much difficulty in recommending his ideas to those less gifted with imagination than himself.